

# INSECTES SOCIAUX

BULLETIN DE L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX



COMITÉ DE RÉDACTION

J. D. CARTHY, P. H. CHRISTENSEN, A. C. COLE,  
K. GÖSSWALD, P.-P. GRASSÉ, C. JUCCI,  
A. RAIGNIER, D. STEINBERG, T. UCHIDA

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NOTES ON INSECTS FOUND IN OR NEAR NESTS  
OF *FORMICA SUBNITENS* CREIGHTON  
(HYMENOPTERA : FORMICIDAE)  
IN BRITISH COLUMBIA (1)

by

Gordon L. AYRE

(Assistant Entomologist. Entomology Laboratory, Belleville [Canada].)

Food habits of the ant *Formica subnitens* Creighton were investigated at Westbank, British Columbia, in the summers of 1954 and 1955. A number of other insects were commonly found within the nests or closely associated with the ants. This paper presents the data collected and observations made on some of these insects. The information presented was collected over a two-year period and was taken from approximately 20 nests of *F. subnitens*.

Except *Crambidia casta* (Pack.), *Cremastocheilus armatus* Wlk., *Medon* sp., and the Aphididae, all the insects found in and near ant nests were attracted by conditions created by the ants rather than by the ants themselves. The structure of the ant nest modified the temperature of the surrounding soil and probably aerated the soil to some extent. This resulted in greater plant growth, which, together with the modified microclimate, created suitable conditions for phytophagous insects. The abundance of phytophagous insects in turn attracted a large number of predaceous insects.

*Crambidia casta* (Pack.).

The pearly footman moth, *Crambidia casta* (Pack.), was the most numerous insect found within the nests of *F. subnitens*. The larvae are dark grey with many plumose setae arising from the verrucae. They are 15 to 20 mm. in length when mature. They feed entirely on lichens on the soil surface. The adults are pure white, have a wing span of 35 mm., and fly at night.

The first-and second-instar larvae were first noted about June 1. Until they pupated in late July the larvae were frequently seen on the ant

(1) Contribution n° 3583, Entomology Division, Science Service, Department of Agriculture, Ottawa, (Canada).

trails and nests but were ignored by the ants. During the heat of mid-day the larvae were commonly found sheltering under stones together with *F. subnitens*. Ants were not observed to attack the larvae. Many of the larvae entered the nests of *F. subnitens* and pupated during the latter part of July. At this time the presence of the ants did not cause them to remain motionless and they were observed to wander in and out of the nests together with the ants. By August 1 all the larvae had pupated in the detritus surrounding the brood chambers of the nests. In laboratory tests the thin, weblike cocoons of the pupae afforded sufficient protection against attack by the ants. Naked pupae of *C. casta* were readily accepted as food by the ants.

The adult moths emerged from the pupae during the morning hours in mid-August. Adults were not observed emerging from the nest and it is not known whether they emerge directly through the detritus or through the brood chamber and the regular openings in the nest. Ants were observed to attack the moths. However, the scales of the moth were repellent to the ants and during the two summers of observation only three were observed captured and brought into the nest.

The exact relationship between *F. subnitens* and *C. casta* is not clear, but their apparent indifference to one another, particularly during the latter larval instars of *C. casta*, indicates that *C. casta* is a synoekete (Donisthorpe and MORLEY, 1945). The ants gain nothing from the relationship and the moth apparently gains nothing directly other than a suitable place to pupate. Indirectly the pupae may gain some measure of protection from parasites and predators.

To obtain information on the latter, three nests of approximately equal size but with colonies of different sizes were dug up and the contents examined. The first nest contained a vigorous colony of average size, the second contained a small but vigorous colony, and the third had been abandoned by ants. This gave a nest with all the detritus inhabited by ants, one with the periphery of the detritus uninhabited by ants, and one with all the detritus uninhabited. All insects other than ants were recorded and all *C. casta* larvae and pupae were reared to maturity. The number of *C. casta* collected and the emergence of adult moths and parasites are shown in Table I.

The number of larvae and pupae of *C. casta* found in each nest was approximately proportional to the number of ants. This would suggest that it is the ants that attracted the larvae. It is also possible, however, that well-aerated detritus that is free from molds, as in a large healthy colony, is more suitable for pupation of the larvae than the decaying detritus found in unattended nests or in nests with low ant populations.

As there was little difference between the three nests in the percentage parasitism by Hymenoptera, it is unlikely that the ants had any influence in preventing parasitism of *C. casta* by these insects. The greater incidence of parasitism by Diptera in the abandoned nest may be of some significance; however, as proved from separate rearings of field-collected *C. casta*



larvae, all Diptera obtained were larval parasites and therefore the ants would be of little importance in preventing parasitism. On the other hand, when the collections from ant nests were made, all the dipterous larvae had emerged and pupated in the detritus; hence, many of the dipterous larvae may have been captured by the ants between the time of emergence from the host and pupation as during this period they are completely defenseless against attack.

TABLE I. — PARASITISM OF *C. casta* REARED FROM THREE NESTS OF *F. subnitens*.

	NORMAL NEST.	PARTIALLY ABANDONED NEST.	ABANDONED NEST.
Number of <i>C. casta</i> larvae and pupae collected.	495	367	46
Number of moths reared.	351	196	17
Numbers of hymenopterous parasites reared.			
<i>Hyposoter ochreofrons</i>			
<i>lexiphaga</i> (Wyl.).	120	83	6
<i>Mesochorus</i> sp.	1	1	0
<i>Ichneumon</i> sp.	2	11	8
<i>Gelis</i> sp.	0	0	3
Unknown (emerged).	8	52	0
Total percentage parasitism by Hymenoptera.	27	40	37
Numbers of dipterous parasites reared.			
<i>Neophorocera edwardsii</i> (Will.).	17	7	1
<i>Pseudochaeta canadensis</i> Brks.	4	0	0
Unknown (emerged).	3	17	11
Total percentage parasitism by Diptera.	4	7	25
Total percentage parasitism.	31	47	62

### *Cremastocheilus armatus* Wlk.

WHEELER (1910) stated that the larvae of this genus of beetles live in the detritus of the nest and, though this species had been taken from nests of *Camponotus* and *Aphaenogaster* spp., he regarded *Formica* spp. as its true host. ESSIG (1926) stated that *C. armatus* occurs in the nests of the black harvester ant, *Veromessor andrei* (MAYR). In these studies only the adults of *C. armatus* were found and these were always captured outside ant nests. In many cases they were taken dead from

the ants as they were being brought to the nest, possibly as food. They were taken alive on only two occasions and then they were being hauled to the nest by the ants. They gave slight resistance to the ants, and either were unable to escape or were reluctant to do so. WHEELER (1910) regarded these beetles as indifferently tolerated or even persecuted synoeketes. Observations made during the current studies suggest the latter is true in relation to *F. subnitens*.

### *Medon (Platymedon) sp.*

This staphylinid beetle was found in small numbers in all nests examined. Little is known of its association with these ants and, as other species of staphylinid beetles may be hostile persecuted lodgers or true ant guests (WHEELER, 1910; DONISTHORPE, 1927), little can be said of their association on the basis of the family as a whole. DONISTHORPE (1927) found *Sunius bicolor* (Ol.) (*Medon bicolor* [Ol.]) in nests of *Lasius flavus* (Fab.) (*Acanthomyops flavus* Fab.) and *Myrmica ruginodis* Nylander but he considered these chance occurrences. *Medon (Platymedon) schwarzi* Blackwelder was recorded by BLACKWELDER (1943) as being taken from under a stone in company with the ant *Odontomachus haematoda* (Linne).

HATCH (personal correspondence) stated that *Medon (Platymedon) shastanicum* (Casey) also occurs with ants. In all cases little seems to be known of the biology of these beetles, and their relationship, if any, to the ants is not known. However, as *Medon* sp. was always found with *F. subnitens* this species appeared to be not merely a chance capture but to have some definite association with the ants.

This species is described in "Beetles of the Pacific Northwest, Part II", by HATCH (in preparation).

### *Carabidae.*

Apart from *C. casta* and ants the most numerous insects taken from nests were *Harpalus* spp. In one nest 123 individuals were found in the detritus. *Harpalus* spp. were always found in the portion of the detritus uninhabited by the ants and they apparently avoided any contact with the ants. When they were exposed they were always attacked by the ants. Their presence in the detritus was probably for food or shelter or both.

*Cymindis* sp., *Amara* sp., and *Stenolophus conjunctus* (Say) were also found in the detritus of most nests but in relatively small numbers. The relationship of *Cymindis* sp. and *Amara* sp. to the ants was considered similar to that of *Harpalus* spp. as they were readily attacked by the ants when exposed. *S. conjunctus*, on the other hand, was frequently found under sticks and rocks together with *F. subnitens* during the hotter parts of the day. This beetle and the ants appeared to be completely indifferent to each other.



### *Scarabaeidae.*

Nests of *F. subnitens* are usually surrounded by luxuriant growths of grass or weeds. These plants, which are often twice as high and dense as those in the surrounding areas, provide excellent feeding areas for many phytophagous beetles. One of the most common species, *Phobetus comatus comatus* Lec., was usually found within two feet of the nest and was taken within one inch of the brood chamber. Approximately 120 larvae of this beetle were taken within a two foot radius of the nest.

Small numbers of *Diplotaxis* sp. larvae and other unidentified scarabaeid larvae also were taken from this area. In all cases the ants were hostile to them.

### *Curculionidae.*

The larvae and adults of the strawberry root weevil, *Brachyrhinus ovatus* (L.), were commonly found in quantities of 50 or more near the nest. The larvae were found in the soil adjacent to the brood chamber whereas the adult were frequently in the uninhabited portions of the detritus. There is definitely no friendly relationship between these weevils and the ants: in the studies on feeding habits of *F. subnitens*, *B. ovatus* formed 10 to 15 per cent of all the observed food intake of the ants.

### *Aphididae.*

Aphids were probably more closely associated with *F. subnitens* than any other insects found, though none were found within the nests. Much has been written on the association of ants and aphids and little is said here other than to list the more important species that supply *F. subnitens* with honeydew.

The species most frequently tended by *F. subnitens* was *Bipersona torticauda* (Gill.), which occurred on a thistle, *Cirsium* sp. These aphids were present in such large numbers that only those on the lower portion of the thistle stems were tended by the ants. Three species of coccinellids of the genus *Coccinella* and two of the genus *Hippodamia* were found feeding on the aphids on the upper portions of the stems. The feeding areas of the ants and coccinellids were not found to overlap.

*Capitophorus fragaefolii* (Ckll.) and *Lachnus rosae* Cholo, both of which occurred on *Rosa* sp., probably supplied the ants with more honeydew than did all other species of aphids. Though they did not occur in the same concentrations as *B. torticauda*, they were more widely distributed. Few ant nests were out of range of rose bushes whereas only a very small number were near thistles. Furthermore, the shade provided by the rose bushes allowed the ants to collect honeydew throughout the day.

The majority of other aphid species occurred in areas where temperatures of the mid-day period became too high for ant activity.

A fourth species of aphid that, when available, apparently supplied the ants with honeydew was *Aphis gossypii* Glover. This species was found only on a small species of legume and, as this plant was not plentiful, the total production of honeydew was not great. Similar situations occurred with *Aphis maidiradicis* Forbes and *Myzus circumflexus* (Buck.), which occurred on the roots of *Helianthus* sp. and of legumes respectively. Their honeydew was acceptable to the ants but because of the small numbers of these plants the total production was not great.

### *Membracidae.*

The nymphs of the membracid *Campylenchia latipes* Say were as important a source of honeydew as were aphids. The nymphs were generally found on the roots and crowns of such plants as *Helianthus* sp., *Tragopogon* sp., and *Achillea* sp. before the flowering stalk was formed. The adults of this species, however, were eaten by the ants.

### *Other insects.*

Many other insects, particularly Coleoptera, were occasionally found in the detritus or around ant nests. However, as these insects were also found in approximately equal numbers in other areas they were not considered to be especially attracted by the ants or the nest.

### *Summary.*

At Westbank, B.C., during 1954 and 1955 the insects closely associated with the ant *Formica subnitens* Creighton were the arctiid *Crambidia casta* (Pack.), which pupates in the ant nest; the scarabaeid *Cremastocheilus armatus* Wlk., which is a known myrmecophile; and the staphylinid *Medon* (*Platymedon*) sp., which was not found away from the ant nests. A group of insects frequently found in the nests but not associated directly with the ants in any way included the carabids *Harpalus* spp., *Cymindis* sp., *Amara* sp., and *Stenolophus conjunctus* Say; the scarabaeids *Phobetus comatus comatus* Lec. and *Diplotaxis* sp.; and the curculionid *Brachyrhinus ovatus* (L.). A third group of insects supplied the ants with secretions but did not live within the ant nests. The most important of these were the aphide *Bipersona torticauda* (Gill.), *Capitophorus fragaeifolii* (Ckll.), *Lachnus rosae* Cholo, *Aphis gossypii* Glover, and *Myzus circumflexus* (Buck.) and the nymphal stages of the membracid *Campylenchia latipes* Say.



*Résumé.*

A Westbank, E. C., pendant 1954 et 1955, les insectes associés étroitement avec la fourmi *Formica subnitens* Creighton étaient l'arctiide *Crambidia casta* Pack. qui se nymphose dans le nid ; le scarabéide *Cremascheilus armatus* Wlk. qui est connu comme myrmécophile, et le staphylinide *Medon* (*Platymedon* sp.) qui n'a jamais été trouvé ailleurs que dans les fourmilières. Parmi les insectes fréquemment trouvés dans les nids mais non associés directement aux fourmis, on rencontre les carabides *Harpalus* sp., *Cymindis* sp., *Amara* sp. et *Stenolophus conjunctus* Say ; les scarabéides *Phobetus comatus comatus* Lec. et *Diplotaxis* sp. et le curculionide *Brachyrhinus ovatus* L. Les insectes d'un troisième groupe nourrissent les fourmis par leurs sécrétions, mais ne vivent pas dans la fourmilière. Les plus importants d'entre eux sont les aphides *Bipersona torticauda* Gill., *Capitophorus fragaefolii* Ckll., *Lachnus rosae* Cholo., *Aphis gossypii* Glover et *Myzus circumflexus* Buck. et les nymphes du membracide *Campylenchia latipes* Say.

*Zusammenfassung.*

Die Insekten, welche in den Jahren 1954 und 1955 bei Westbank, British Columbia, mit der Ameise *Formica subnitens* Creighton zusammenlebten waren die Arctiide *Crambidia casta* (Pack.), die sich in dem Ameisenhaufen verpuppt ; die Scarabaeide *Cremascheilus armatus* Wlk., die ein bekannter Ameisengast ist ; und die Staphylinide *Medon* (*Platymedon*) sp., die nicht außerhalb von Ameisenhaufen gefunden wurde. Eine Gruppe von Insekten fand sich häufig in dem Nest, war aber durchaus nicht fest an die Ameisen gebunden : die Carabiden *Harpalus* sp., *Cymindis* sp., *Amara* sp., und *Stenolophus conjunctus* Say ; die Scarabaeiden *Phobetus comatus comatus* Lec. und *Diplotaxis* sp., und die Curculionide *Brachyrhinus ovatus* (L.). Eine dritte Gruppe von Insekten versorgten die Ameisen mit Sekreten wohnten aber nicht in dem Ameisenhaufen. Die wichtigsten von diesen waren die Blattläuse *Bipersona torticauda* (Gill.), *Capitophorus fragifolii* (Ckll.), *Lachnus rosae* Cholo., *Aphis gossypii* Glover, und *Myzus circumflexus* (Buck.) und die Nymphen der Membracide *Campylenchia latipes* Say.

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# OBSERVATIONS ON THE BLACK TERMITES, *HOSPITALITERMES* SPP., OF JAVA AND SUMATRA

by

L. G. E. KALSHOVEN

(Blaricum, Netherlands)

... eine Termitenform von ganz aussergewöhnlichem  
biologischen Interesse...

ESCHERICH, 1911:121.

In 1934 KEMNER published his description of *Hospitalitermes diurnus* based on material submitted to him by the present author. The specimens had been collected in a teak forest of the Semarang district in Central Java in May 1921 shortly after I had been appointed forest entomologist at Bogor. The peculiar openly-moving columns of this termite (Plate A) were seen rather frequently on duty tours in the forests in subsequent years but very little time could be spent on close observation. However, the few notes made at different times may be of interest as so little has been published on the Indonesian representatives of the remarkable genus whose distribution is confined to the Indomalayan and Papuan regions.

A digest of all the particulars on the biology of *Hospitalitermes* which could be found in the literature is given first.

## A. PUBLISHED RECORDS

### *Observations in Ceylon.*

*Hospitalitermes monoceros* Kœn. of Ceylon is by far the best known species of the genus. KœNIG who discovered and described it as early as 1779 added a few notes on the nest site only. NIETNER (1857), a resident of Ceylon, was the first to mention the openly moving columns. His later personal communication to HAGEN (1860, p. 78) contained a few details on the nest structure and its inhabitants. A small sample of the nest substance, included in the consignment received, enabled HAGEN to comment on it (p. 117).

In 1899 W. HORN visited Ceylon and collected material, which was identified by WASMANN (1902), who gives a few particulars about two nests found in tree crevices (p. 130).

For several years BUGNION spent the winter months in Ceylon (cf. ESCHERICH, 1911) and became greatly interested in termite life especially in that of 'Le Termite noir'. In his first notes (1909 *a*, *b*) he gives his observations on the trail forming, the method of defence of the nasuti and the possible kind of food, and he describes the situation of two nests, one in the roof timber of a shed and the other in a hollow trunk in the jungle. The latter nest was opened and the queen was found in a small hole on the bottom.

In a second contribution (1910), dealing with other termites also, BUGNION rectifies a few of his earlier interpretations of the action of the offensive fluid produced by the nasuti; he mentions a peculiar nest odour and the occasional feeding of workers on dead leaves.

ESCHERICH paid a visit of 8 weeks to Ceylon for his termite studies in January-March 1910; he stayed a few days with BUGNION and spent 6.5 weeks in Peradeniya where he was assisted by the entomologist GREEN and the mycologist PETCH, who were on the staff of the experiment station and had already been engaged in termite studies. ESCHERICH became quite fascinated by *H. monoceros*, 'die schwarze oder Kot-Termite', to which he devoted 23 pages in his book 'Termitenleben auf Ceylon' (1911). Here he gives a vivid description of the marching columns with their many detours, the defensive as well as the scouting rôle of the nasuti, the mutual grooming activities of the nest associates, the method of communication of alarms, the building of nest partitions with stomodaeal and proctodaeal secretions, and the division of labour between the feeding workers and the individuals which carry the material to the nest. His remarks on trail marking with proctodaeal specks and his explanation of the rather loose and crumbly outer part of the nest as a mass of faecal matter are convincing.

In a detailed and ample discussion of ESCHERICH's book WASMANN (1911) called the termite 'eine Wandertermiten'.

A third paper of BUGNION (1911) again deals exclusively with *H. monoceros*. A complete nest was placed on a verandah whereupon the colony soon began to forage on lichens on the trunks of coconut trees in the adjacent plantation. After a second nest had been placed in the same room a severe fight ensued but, finally, the colonies merged and dense foraging columns were formed. The author gives a record of observations from 21 December 1910 till 8 March 1911 which shows that the harvesting expeditions were made daily. Groups of varying size were occasionally seen feeding also on the humus (black earth) of a flower bed. This was repeated 7 times in one particular period of 23 days. Feeding was observed also on algal growth on a roof and a foundation wall. Successful manœuvres against the predatory ants, *Ecophylla* and *Pheidologeton*, are recorded.

Later papers of BUGNION have not added any new details on the matter (1913, 1922).

GREEN in his termite catalogue of Ceylon (1913) gives only the barest details on the nest sites and the processions of *monoceros*.

The Russian termitologist O. JOHN visited Ceylon soon afterwards, in November-December 1912 and *H. monoceros* is dealt with at some length in his first notes about his observations (1913). He expressed himself as being critical about the observations of the division of labour between the workers as mentioned by ESCHERICH and BUGNION and about the former's explanation of the significance of the 'Zitterstosze'.

In a short 'Reisebrief' of another visitor, VON BUTTEL REEPEN, written from Ceylon (Jan. 1912) and apparently meant as a preliminary note, it is stated that *monoceros* could only be studied superficially. The fact is stressed that indigested wood particles were found in the 'Kot-Stalaktiten'.

PETCH, in his search for fungi cultivated by termites, did not detect any on the nest material of the black termite, of which he investigated a far larger number of nests apparently than BUGNION or ESCHERICH. In a complete description of the nest in his well illustrated paper (1913) he particularly enlarges about the structure and meaning of the outer 'stalactitic masses hanging from the inhabited hollow trunks and decaying branches'. They are constituted of loosely adhering faecal pellets and are regularly washed away by heavy rains, a process observed in one nest for three successive years. Fragments of wood are incorporated in the matter sometimes when too much of the material has become detached. The nest proper is a comb built of a different amorphous matter and occupies cavities in the branches and stems. These combs may be as long as 20 feet (6.5 m) in narrow cavities. The normal position of the parent couple is in the centre of the nest but there is no concentric structure nor a thickwalled cell.



—Another paragraph deals with the 'organized processions in search of food' and gives many interesting new details on the course of the tracks with their detours, the delays as a result of disturbing conditions, etc. PETCH concludes that algae are preferred as food but, as their supply is limited, lichens are the staple food. However, only lichens of a particular crustaceous type and in a particular stage of development are consumed.—Very interesting observations were made on a large colony which had left their original nest after this had been taken down and split up indoors. After wandering about the laboratory they finally took possession of a flower pot covered with a bell glass. Here they began to construct a nest using sand particles cemented with stomodaeal glue as well as semi-fluid anal secretions. The colony made nightly excursions and was provided with a yellow brown alga for three months.

In a list of the pests of cultivated plants in Ceylon (Anonym, 1923) '*Termes*' *monoceros* is mentioned under *Cassia multijuga* and *Ficus religiosa*. The first reference is not clear but the latter may well concern the occurrence of a nest in the base of a tree.

### Observations in the Philippine Islands.

A black termite called 'anay-maitim' not nesting in the ground but moving in the forests was reported from the Philippines already by HAGEN (1860, p. 82). This may have been the common *Hospitalitermes luzonensis* which has since become known from the region, and not a *Lacessitermes*.

A most readable account of this black termite's regular visits to an old building in

FIG. 1. — Part of descending, nest-bound column of *Hospitalitermes luzonensis*. Three workers carry a bunch of forage, five nasuti on guard along the flanks. Sketch by F. X. Williams, 1928.



the forest was given by F. X. WILLIAMS in 1928. He described the way the columns leave their nest preceded by scouting and guarding nasuti, and mentions many more interesting details (text-figure 1).

LIGHT must have been unaware of WILLIAM's note. In a paper of 1930 he mentions only incidentally that *Hospitalitermes* makes 'extensive forays in searching for food'. In his study on 'The nasute termites of the Philippines' (1936) he emphasizes the presence of one single highly variable *H.* species in all parts of the archipelago and adds this note: 'Its armies extend for a distance of at least several hundred yards, consisting of five or six lines of workers, flanked by an outer cordon of soldiers. They gather fragments of decayed leaves, possibly of fungus, which are taken to the nest, a large dark brown structure at the base of a tree giving off an unpleasant odour. This

species, whose nests are to be found by careful search almost on the outskirts of Manila, offers a remarkable opportunity for a study of social organization, caste determination, feeding methods, behavior, etc.'

The Philippine entomologist PANGGA (1936) has given a few more data on the species, from which the following may be quoted: 'Places covered by grass were preferred (by the columns). Heat of the sun may be one of the factors that affect the duration of the travel. In the forest where the ground is shaded, it was found that they travelled the whole day, while in the exposed places open foraging ceased when the sun rays grew warm enough to dry the dew. The soldier: worker coefficient in a sample collected from travelling bands was 0.11.

MORRIL (1953) in his 'Army insect operations in the Far East' has recorded that 'control was called for by persons on whose mango trees nests were being built by.... *Hospitalitermes luzonensis* Oshima although the termites did not cause any apparent injury'. This record leaves room for a good many questions.

### *Observations in Borneo, Malaya, Sumatra and Java.*

HAVILAND (1898) presenting his 'Section with *Termes hospitalis* for Type' states 'The termites (of this group) traverse the jungle in long troops, which may be met returning any hour till midday, the workers carrying each a ball of food in its mouth'. Of *T. hospitalis* it is mentioned that the nests 'generally occupy the centre of the nest of *T. comis*, and have large entrances at the upper part'.

In 1904 an easily overlooked note about *H. umbrinus* in Malaya appeared in a report of C. ROBINSON. It runs: "This species nests in the stumps of dead trees and is often seen on the march in enormous numbers, frequently travelling a distance of two or three hundred yards in columns a couple of inches wide. It apparently feeds on dead leaves, twigs, etc., and is occasionally seen in houses situated near jungle, but does not do any harm". The same report was again printed in 1905. In a note of the editor to the first issue of the report, H. N. RIDLEY comments: "the workers collect scrapings of algae and fungi apparently". This may have been a correct observation. His further remarks about the species being a fungus grower and about the decay of trunks and timber supposedly caused by the nests must be considered incorrect.

HOLMGREN (1913) in dealing with the termite material collected by the able Dutch amateur entomologist E. JACOBSON, identified a *Hospitalitermes* from the locality 'Djokja' as *H. bicolor* Hav. Jogya (more correctly written Yogyakarta) is the name of a province in C. Java and of its capital. It is almost certain that JACOBSON got this specimens in a teak forest in this province, which is in close proximity to the type locality of *H. diurnus* Kemner 1934. An accompanying note of JACOBSON, reproduced by HOLMGREN reads 'Diese Termiten sah ich mitten am Tage marschieren, sie kamen zwischen den Luftwurzeln eines Baumes hervor und war die Kolonne 20 M. weit zu verfolgen, bis sie sich im Gebüsch verlor. Auf kurze Strecken lief der Kolonnenweg in der vollen Sonne. Die Kolonne war 1 bis 6 Termiten breit. Hier und dort standen an den Flanken Nasutisoloden still. Das Nest konnte ich nicht finden'.

In his later taxonomic studies of the termite material collected by von BUTTEL REEPEN in Ceylon, Sumatra, Malaya and Java, HOLMGREN (1914) inserts the remarks 'grosse Heereszüge, Flechtensammler' against *H. hospitalis* Hav. and *H. hospitalis* f. *mediosflavus*. After *H. umbrinus* f. *sharpi* he inserts the collectors note: 'Heereszüge im Dschungel. Fäcesnest ähnlich wie das von *E. monoceros*, aber nicht schwarz, sondern braun in hohlem Baum (Malacca). Dagegen schwarzer Bau (Soengei Banban, Sumatra). Ueber interessante Abweichungen mit dem von *Eut. monoceros* siehe Reisebericht'. Most regrettably this 'Reisebericht' to which HOLMGREN often refers has remained unpublished.

JOHN (1925), discussing his views on termite biology obtained during his S.E. Asian collection trip, connects the feeding of *Hospitalitermes* species on lichens with the more general use of fungal mycelium as food (p. 376-377). He briefly describes a nest of



*H. bicolor*, formed in a hollow tree and provided with large 'Kotstalaktiten' and he mentions another colony found in a nest of *Termes rostratus*, both in E. Sumatra. He came across *H. umbrinus sharpi* nesting in a hollow trunk and grazing the bark of a tree in Malaya, and inhabiting the nests of *T. rostratus* in Sumatra. He reproduces a note by the myrmecologist KARAWAYEW, who found the species in Depok (W. Java, between Jakarta and Bogor) between the roots of a large tree, 12.1912. (The latter

FIG. 2. — Sketch of nasute of black termite of N. Sumatra. From Heusser, 1926.



locality included a small reservation of lowland jungle forest. KEMNER and other entomologists collected in the same place but did not find the species any more).

Of *H. hospitalis* JOHN states that its nests occur in hollow trunks and similar places, and that the species is often associated with *T. rostratus*, *comis* and *laticornis*. A rotten hollow stump with a cap built by termites was occupied simultaneously by colonies of *H. hospitalis*, *Termes rostratus* and *Rhinotermes longirostris*. Furthermore he mentions the finding of a colony of *hospitalis* coinhabiting with a colony of *T. laticornis* and one of *Melipona* bees in an irregular spherical nest of  $88 \times 65 \times 57$  cm built on a very strong branch overhanging a brook. This appears to be in contradiction to



FIG. 3. — Column of black termites, spreading on basal part of rubber tree to forage on the lichens. Sketch by Heusser, 1926.

JOHN's assertion that the *H.* species build their nests in hollow trees and the like, which observation is in agreement with those of all other authors. Perhaps in this case the nest had been built originally by a truly arboreal termite species and had been occupied afterwards by *Hospitalitermes*.

The occurrence of groups of rubber trees in plantations in N. Sumatra showing an uncommonly smooth and dark green bark, led to the discovery by a botanist (HEUSSER, 1926) that the phenomenon was due to the removal of the thin cork layer covered with lichens by feeding ant-like insects. They proved to be a black termite which had its nests in a rotten log and was identified as *Eutermes* sp. A sketch published

of the nasutes and worker suggests a *Lacessititermes*, but the details of the antennal joints may not have been sufficiently accurate and the situation of the nest points to its being a *Hospitalitermes*. A short description is given of how the termites move by night and arrange themselves in groups on the feeding grounds (text figures 2 and 3) depriving the trees from their cork layer, first at the base and gradually working up to the branches of one inch in diameter only.

A *Hospitalitermes* found by JACOBSON in W. Sumatra was identified by KEMNER (1930) as *H. medioflavus* Holmgr. The author adds the following explanation taken from the collector's letter: "Die Nester dieser Termiten fand ich an senkrechten Felswänden angeklebt. Es sind flache unregelmässige Kuchen mit unebener Oberfläche, durch mehr oder weniger breite Gänge verbunden; unter diesen Kuchen leben die Termiten. Die königliche Kammer und ihre Insassen habe ich noch nicht finden können, vielleicht ist dieselbe unterirdisch... Die Arbeiter dieser Art fand ich in den in der Nähe befindlichen Gambirpflanzungen (gambir = the tanning matter produced by *Uncaria gambir*), wo sie die Flechten (und die Rinde?) der Gambir Strauchen abnagten und in der Gestalt kleiner Kugeln nach dem Neste schleppten".

After *H. diurnus* had been described by KEMNER (1934), the following note was published in my paper on the Javanese termites (1936) (transl. 'A brown species (of day-foraging termites) is commonly to be observed in the teak forests and makes its nest under tree stumps and hollow trunks. The nest site, if not indicated by columns of termites streaming into or from the nest, is recognisable from the mass of granular, black material piled up on the outside and formed by faecal matter. The inner structure has not yet been investigated').

The investigation of the inner structure of the nest and the search for the parent couple was carried out in 1940-1941 by the Javanese assistants at the field laboratory MAS SUDIRO KARTOHADIBROTO and Mantri WARNODIHARDJO upon the instigation of Ir P. A. BLIJRDORP then acting as forest entomologist. The main details which came to light may be found in BLIJRDORP's paper of 1941.

A short excerpt from the publications of HEUSSER and BLIJRDORP and from my own observations appeared in my book on the 'Pests of the Indonesian Crops' in 1950.

SCHNEIDER has mentioned a broad trail of termites carrying their balls of lichens, which he encountered on one of his trips through the Sumatran jungle near the Asahan river (1941).

## B. NEW RECORDS ON HOSPITALITERMES FROM JAVA AND SUMATRA

**Identifications.** — The material at hand consists of some 50 samples and several field notes partly illustrated by photographs, most of them collected during my forest entomological duty tours in Java, with additional material from Ir P. A. BLIJRDORP and Mr. Fr. A. H. Th. VERBEEK.

Dr. W. V. HARRIS of London has been kind enough to examine some 30 assorted samples and to give his opinion on the identity of the species.

All the material gathered near the field laboratory in the teak area of C. Java (at the train stop Gedangan, district Semarang), forming the greater part of the collection and including alates and dealates was identified as *H. diurnus* Kemn., which is considered by Dr. HARRIS to be "a better species than many others". It appears to occur also in the forest areas of the districts Pekalongan, Japara, and Rembang—all along the N. coast of C. Java—and on the Isle of Banka (leg. J. van der VECHT, Petaling, 2.1932).



In the forests of Pekalongan another species besides *diurnus* appeared to be present, viz. *H. ferrugineus* John, originally described from E. Sumatra.

The samples from Banjar, W. Java, with its wet climate, belong to *H. umbrinus sharpi* Holmgr., first described from the Mal. Peninsula and recorded by JOHN also from E. Sumatra and from Dépok, W. Java.

Dr. HARRIS felt unable to give a specific name to the single sample from South Sumatra, because—as he wrote—10 species have been described and recorded from that island and the genus really wants to be examined carefully as a whole.

The author wants to express again his sincere thanks to Dr. HARRIS for his highly appreciated assistance.

**Vernacular names.**—The dark-coloured, openly marching termites have a name of their own in certain districts of Central Java, viz. 'sumpyoh'. In W. Java the openly moving dark species, including those of *Lacessitermes* have the name of 'pua item', in which item = black, and pua is the name for *Nasutitermes* species collectively. In S. Sumatra the name 'anay item' has been met with (anay = termite). All this may be considered another proof of the perceptive faculty of observation of the Indonesian country people and their familiarity with animal and plant life. They never take the black termite for ants. Indeed, they never have mistaken termites for ants as is so commonly done in the tropics by western visitors and settlers.

### **Observations on *Hospitalitermes diurnus*.**

**Foraging activities.**—The main activities abroad of the sumpyoh take place during the night as is the case with other *Hospitalitermes* species, the termites beginning to start from their nests at dusk and leaving the feeding places the next morning, meanwhile keeping up a steady stream from and to the nest. People working in the forests will mainly see the home-bound streams, which are often still on the move at 8-9.30 a.m. and even later.

In the forest thickets the symphyoh preferably moves at some distance off the ground, trailing along fallen branches, the bases of trunks, stalks and stems of shrubs and other vegetation etc. It is evident that as a rule they cannot follow straight lines for an appreciable distance under these circumstances and almost continuously have to deviate from their main direction. Besides they very often make long, apparently unnecessary detours in the shape of large loops, or climb a stump or tree trunk to some height only to descend along a parallel line on the other side. These 'irrational' detours have struck all observers of the *Hospitalitermes* columns. However, the sumpyoh termites are not averse to following open paths or to cross glades if necessary, moving on the ground

itself (Plate A 1, 2). In teak forests under management they have often been seen travelling along the inner side of the rails of narrow-gauge tracks (for timber transport); in one instance they were observed moving along a small pipe line of an oil company in the forests near Tjepu and they were also seen crossing a zinc rain pipe between two buildings on the premises of the field laboratory at Gedangan.

In the homeward-bound columns the greater part of the workers may be seen carrying the small greyish or brownish bunches of collected material; sometimes light and darker coloured material is carried by different workers in the same group.

The actual feeding activities have been witnessed by me only a few times. Once a colony was busy on young trees lying in a thinned out plantation of mahogany where they were feeding on decorticated parts of the poles, and to a lesser degree on some bark covered places. With a 16 x lens it was seen that fibers were standing out from the grazed-over surface of the wood, indicating that the wood fibres had been torn by the termites while collecting their material. Furthermore it was noticed that workers were adding their bits to the pile carried by other individuals. JOHN is the only investigator who failed to see this division of labor and doubted the correctness of ESCHERICH's statements. On other occasions the symphyon were observed foraging on the upper side of the teak wood shingles of the roof of the field laboratory and a few other parts of the timber exterior of the house (Plate A, 4).

A similar instance of feeding on the surface of structural timber has been recorded by WILLIAMS, who aptly described it in these words (p. 67, 68): 'the objective (of an out going stream) was a large beam along the wall of the room along which they spread from end to end. Here and there workers collected in groups, biting off tiny splinters and chewing them into a pulp. . . . The numerous chewers of wood. . . are intent upon their work, heads applied to the perfectly sound wood, whether it be the beam or the bamboo flooring. Tiny splinters appear and soon a masticated mouthful is collected. Sparse among the mass of termites, workers carrying large and small loads stand around or walk about a little. . .' etc.

PETCH reporting on a single case observed of the black termites feeding on the surface of wood of window frames blackened by a fungus, stated that the workers removed a thin layer of wood which contained the

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PLATE A. — 1. Columns of *H. umbrinus sharpi* dividing and merging again while traversing a stony path, 2. idem ascending the exposed roots of a tree. 3. Column of *H. diurnus* returning to nest under a large trunk. 4. Group of *H. diurnus* foraging on the outer side of a beam which supports the floor of a wooden building. 5. Large descending column of *H. diurnus* halting on a wooden post (tarred at base, the rest whitewashed) in the field laboratory, indoors. Note the central path left free for slowly moving individuals, and the fringe of nasuti. 6. Dense column of *H. umbrinus sharpi* crowding on base of large tree on their nestbound move, at noon. The granular appearance is due to the pellets of forage carried by most of the workers. In the middle a path with moving individuals.





mycelium. The fragments were only one cell thick, so thin that the balls appeared almost white.

An additional observation of interest in this connection is the following: After the visit by night of a large symphyoh colony to the field laboratory where they mainly fed on the upperside of the teak shingles it appeared that two groups had fed on the surface of the floor in a room inside the house (further details on this visit are given in the paragraph on the delays). Two moist, slightly roughened spots left by the termites were proofs of their activities. These spots were broadly oval in shape, measuring  $12 \times 3.5$  and  $10 \times 2$  cm; they were situated at 1.25 and 1.50 m distance from the base of the post in the wall which they had used for two successive nights to reach the roof. Most noteworthy in this case is the termites' capacity to feed on the outermost, scarcely weathered layer of sound teak where no algae or bacterial life could be present. No less remarkable is the moistening of the grazing surface by the termites, a feature not mentioned before in the literature and which might be rather difficult to observe under outdoor conditions.

Here the question may be asked, whether regular visits of *Hospitalitermes* may contribute to the gradual reduction in thickness of the teak shingles. The wearing away of these shingles after long service, which makes them so thin that they must be replaced, is a well known fact. In my opinion the main cause lies, however, in the combined actions of micro-organisms disintegrating the surface of the wood, and of rainwater. It is very striking too, that a grating of teak wood used on the floor of a bath room will get smooth corners and edges after some time, and even lose quite a part of its volume in the long run.

The habit of *H. diurnus* to extend its expeditions to houses has been recorded also from the Cocoa Estate Ngobo (October 1937), which is situated near the teak forest border in Central Java (communication of Dr. J. G. BETREM).

**An all night observation of a foraging colony.**—In the files at my disposal is a short report written in the Malayan language by Mantri WARNO-DIHARDJO about an observation carried out with his helpers on the outdoor activities of a colony of symphyoh during the night of 13-14 May 1941. This colony inhabited an old, half rotten teak stump (nr. I in text-figure 4)—50 cm in height, 30 cm in diameter—in a teak stand near the field laboratory.

The termites began to appear at 5.-p.m.; at first they lingered around the exit opening but were soon filing off and circling over a larger area on and around the stump. At 5.15 two columns had been formed, one directed north to stump II—another teak stump 40 cm high and 19 cm across—the other directed southward. The termites of the former column entered stump II but reappeared and finally merged into the southbound stream, which moved toward the base of a living tree teak tree (nr. 1), covered with 'lumut' (a javanese term for fine moss forming a coating or green

film). At 5.30 alates began to come out of the nest (see paragraph below on swarming) but this did not delay the march of the column and at 7.- the files were still on the move. At 8.30 a light rain began to fall for some time. When observations were resumed at 3.- a.m. the column had extended to the teak trees nrs. 2 and 3. The termites were very active, making their rapid oscillating movements and a soft crackling noise could be heard (described in the report as 'tik-tik, tik-tik') apparently made by the feeding on the lumut cover on the dry bark or odd pieces of rotten wood nearby. Part of the workers were already returning toward the nest along the trail carrying their minute bunches of collected material but there were also workers among the returning individuals which did not carry a load but had their 'belly' tightly filled ('perutnja minti-minti'). At 6.- a.m. the larger part of the crowd was on its way home and at 6.30 they had nearly all left the foraging places on the bases of the teak trees. At 7.15 the return, which had looked as if it was speeding up, was still in evidence. At 9.- all termites had vanished into stumps I and II.

Two points of particular interest in this account, viz. the sound produced by the feeding termites and the partial consumption of the food on the spot, are corroborated by observations of PETCH on *monoceros*. This author wrote (p. 414): 'When thousands of them are scraping away the lichen at the same time, a rasping sound can be heard distinctly', and (p. 415) 'Apparently the workers when collecting food eat what they require, and then carry a further supply home'. What appears to be new in the account is the apparent extension of the nesting colony over two stumps (see further below in the paragraph on Nest site and structure).

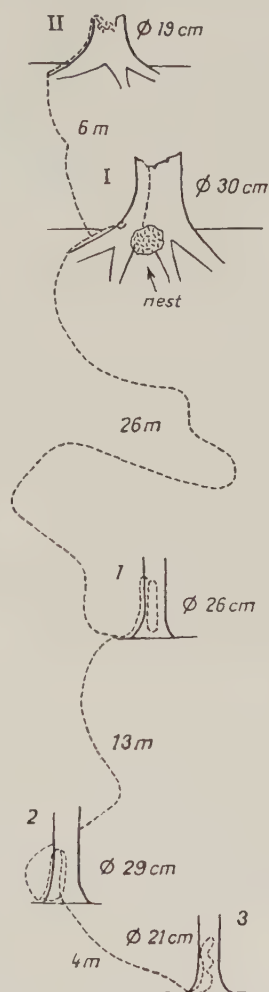


FIG. 4. — Foraging expedition of *Hospitalitermes diurnus* in teak forest, Java. Sketch by Mantri Warno.

**Delays in the return to the nest.**—Observers of the columns of the black termites have sometimes mentioned a temporary halt in the movement, apparently as the result of disturbances or other adverse conditions during their marches (marauding ants, a car passing the track, rain, the heat of the sun, etc.). Two instances observed by me in Central Java will be related here.

In the month of August—therefore in the midst of the dry season—a sumpyoh group was seen moving rather slowly in a thin file on the floor

of a teak stand at 11.- a.m. They were hiding beneath fallen teak leaves on the crumby surface and in the crevices of the clayed soil, which was still humid. The movement was directed to a place at some distance covered with a thick litter of the large teak leaves. No entrance of a nest could be found. Perhaps the colony had fed on the dead leaves.

Another observation, in March 1927, is much more interesting. Rising at 6.30 soon after day break in the guest room of the field laboratory I saw a big column of symphyotermes indoors, streaming down a post of the whitewashed wall. Many workers were carrying their little bunches of collected material. It appeared that dense groups of the termites were still present on the upper surface of the teakwood shingles of the roof. The stream left the room through an opening between the boards near the wooden floor, descended a supporting pillar, traversed a stone path, ascended the wall of a small wooden office, followed the ridge of the roof, crossed to a branch of a large *Ficus elastica* tree which was in contact with the roof, moved along a thick branch of the crown and down the trunk and vanished into a hole near the base of the tree. A large black crust of faecal matter was present here. A much smaller thin column of the termites had its own route from the pillar across the stone path, and moved directly towards the base of the tree over the ground.

On my return to the laboratory at midday a large group of the black termites was still present in the room, crowded over some 75 cm of the lower half of the post in the wall. A path was left free in the middle of the crowd and a few individuals were moving over it. The rest of the group scarcely moved. Only a few of the workers were carrying a load. The occupied part of the white post looked as if moss-covered. A photograph (Plate A, 5) was taken at 1.- p.m. At 3.- the number had decreased and the group occupied a lower part at 30-40 cm above the floor. At 6.-/6.30 p.m. the group of stragglers was much smaller. Then, at 7.45 a new stream appeared moving upward again, and at 9.- the stream had grown into a dense one. Next day at 6.30 a.m. a thin stream was returning nest-ward along the wooden post in the room.

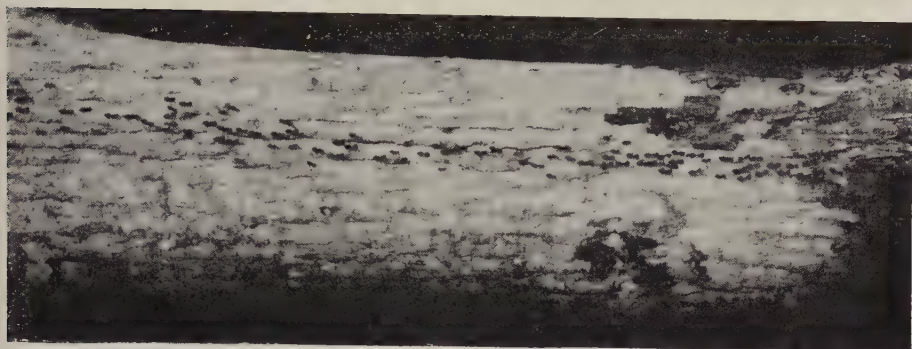
This delay may well have been caused by people walking on the path along the house, and by the heat of the sun.

**Interruption of the trail.**—BUGNION (1909, p. 272 and note a) observed in his first paper that the *monoceros* files leave black marks on their path which apparently enable them to distinguish by their olfactory sense a trail once it is formed. When their path was swept a great disturbance in the column ensued. ESCHERICH made additional observations on this

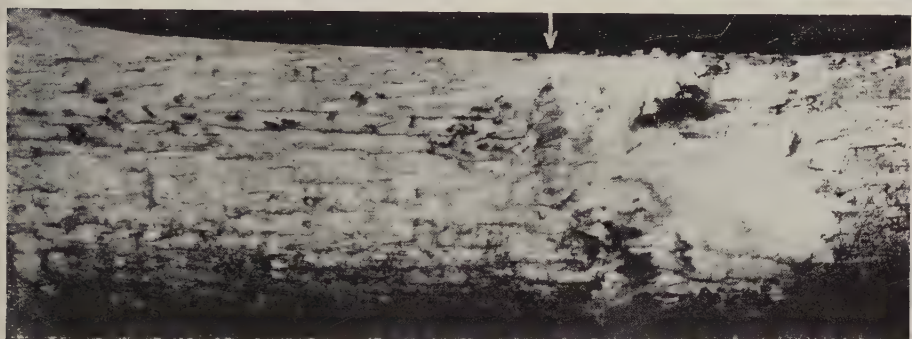
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PLATE B. — Experiment with the interruption of a track of a nestbound column of *H. diurnus* moving from the left to the right over the rough, greyish bark of a young felled teak tree. 1. Before the interruption; 2. column stopping and retreating from place where the bark has been scratched; 3. and 4. the move has started again, the column does not cross the line however but it has split to circumvent the obstacle.

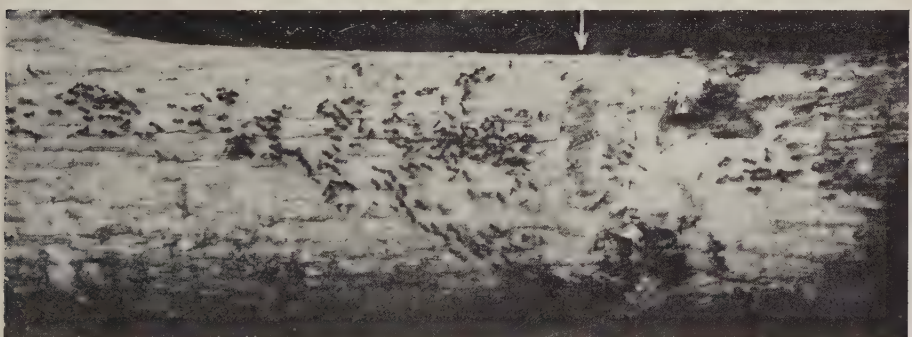




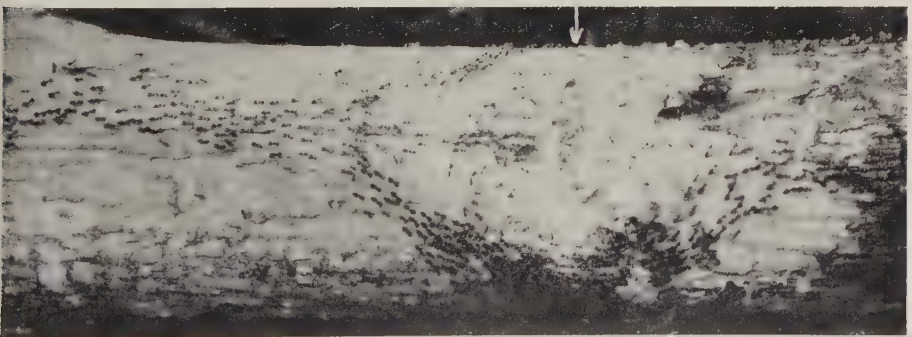
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2



3



4

laying and following of the track. By passing a finger firmly over a trail on the ground the march was immediately interrupted and the trail had to be restored anew, whereby the scouting nasuti advanced first very cautiously (p. 102). He found that the marks were made with proctodaeal matter and published photographs which clearly show the ribbon of dark specks; this track is considered by him as more lasting than the scent trail of ants (p. 115 e.s.).

A similar visible trail has not been observed in the paths of *diurnus* in C. Java, not even where they stream along the bleached surface of an old teak stump (Plate A, 3) or over a white-washed wall (Plate A, 5). Still their track forming must surely be based on the same principle as in *monoceros*. Apparently the fluid secretions of the workers are colourless. Simple experiments have been made by me also with the interruption by a finger or even a pencil stroke of nest-bound columns speeding along a felled tree pole. Immediately the stream stops before the line, showing that the obstacle is vividly perceptible to them though invisible to the observer. The workers shrink from the front line and gradually the nasuti come into action. It was observed that a new connection could be made to circumvent the interruption as is shown in the photograph-series (Plate B, 1-4).

**Swarming, and foundation of new colonies.**—Alates of *H. diurnus* have been caught repeatedly on the lamps in houses standing in the vicinity of teak forests, in lighttraps hoisted into a tree to a height of 20 m (to capture alates of *Neotermes tectonae*) and once on a lighted screen (erected during investigations on the distances covered by swarming *Neotermes*).

In comparison with the large size of the colonies the numbers caught in this way were rather small, always less than a score and often only a single or two specimens. There has been no indication that nests swarm simultaneously over a large area.

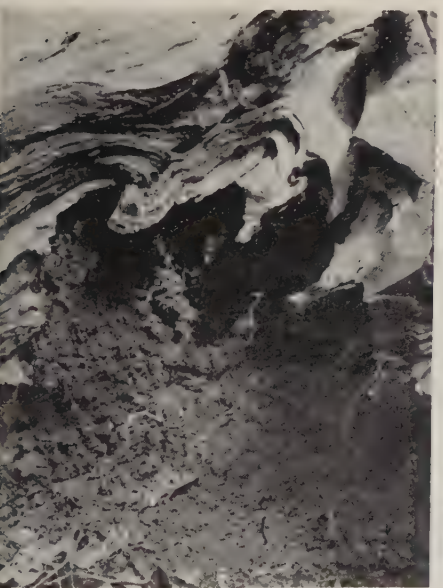
Most dates of alate captures in 1926 to 1928 in the districts Semarang and Rembang in the teak area of C. Java, fall in the period between the last week of November and mid January. There is one specimen, however, dated Gedangan (site of the field laboratory) 10.3.1930, and a sample of 14 specimens dated Tjepu 15.5.1928.

The swarming of the nest near the field laboratory on 27.11.1927 mentioned above and observed by Mantri WARNODIHARDJO, was described in his report in this way (transl.): 'About 5.30 p.m. alates began to come out of the nest. At 5.40 they were moving in the midst of the crowd of workers and nasuti near the exit opening and many of them followed the outbound column. At 6.- the alates on the nest flew into the air all

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PLATE C. — 1. Crust of faecal matter along cleft in teak trunk inhabited by colony of *Hospitatermes diurnus*. 2. Nest of *H. diurnus* in base of old, fire-damaged teak tree. 3. Ditto built in hollow stump. 4. Situation of nest of *H. ferrugineus* in hollow basal part of big *Ficus* tree. F. Verbeek, collecting a sample.







together. Those following the trail were seen gathering into a group ('grombol-grombol') to rise into the air soon afterwards. At 6.40 alates had stopped to emerge from the nest.

This is the first record, apparently, of the swarming of a *Hospitalitermes* colony.

A few times dealated pairs have been found in dry and rotten branches at some distance from the ground on standing teak trees. This occurred during an intensive search for young *Neotermes* colonies, which establish their colonies in the same places. In all specimens of these pairs the apical joints of the antennae were missing, 8-10 joints being left only. No eggs or young brood were found present with them. The way in which the young colonies establish themselves and make their first excursions abroad is still a blank page in the recorded life history of the black termites.

**Nest site and nest structure.**—The nests of *H. diurnus* appear to be of much the same type as those of *H. monoceros* in Ceylon. In the teak forests of Java they are found mainly in the hollow parts of big stumps—still planted in the ground or uprooted already—and of standing trees, especially in those of *Ficus* spp. with their many clefts and crevices in the broad base. In the latter cases the black stalactites of faecal matter often clearly indicate the presence of a nest (Plate C). "Occasionally colonies of these Termites may also be found in worked up and partly buried wood such as in sleepers and posts" (BLIJRDORP, 1941).

Particulars are available on the position of 5 nests of *diurnus* investigated by Mas SUDIRO and mantri WARNO on the instigation of Ir BLIJRDORP. One was located after following a homeward trail for 65 m. The colony was housed in an old hollow trunk standing on the steep border of a brook. After the trunk had been split the nest was found to fill a cavity of 73 cm in height and 56 cm in width in the lower centre of the stump.

Another nest-bound stream followed for over 20 m led to a nest in an old teak stump, 27 cm in diameter. When this stump had been uprooted and split a comb was exposed 20 cm high and 40 cm wide. According to the sketch made at the time the comb extended for 10 cm below the stump, being there in direct contact with the soil.

A third nest was traced after a returning column had been followed in the early morning of 9.3.1941. It passed from a teak stand over a distance of 2 m to a railway, trailed along the rails for some 56 m, traversing a wooden bridge on the way, and then bent off over a distance of some 10 meters to a half rotten teak stump, 55 cm high and 30 cm in diameter. The termites climbed the stump up to 25 cm and entered at a place where the dead bark was rather thin and looked like having been partially eaten. The trunk was excavated with care and afterwards lifted with a lever. The fully exposed comb was situated between the base of two main roots close to the stump. The structure measured 25 cm in height and 20 cm in width. Its lowest part was at 30 cm below the soil level.

The nest of the colony used for the all night observation on 13.5.1941

as related above, was investigated the next day. After the excavation and lifting of trunk I (text figure 4) a comb of  $10 \times 11$  cm was found on the underside. Trunk II, also excavated, lifted and split in two parts, was described as empty, containing only store rooms ('tjuma kedapetan gudang makanan').

As regards the latter interesting observation it may be stated that apparently no store room of collected material has been found by other investigators. However, PETCH mentions the finding of 'a compact cylinder, 50 cm long and 7 cm in diameter, composed entirely of balls of lichen bound together by white mycelium, on the bottom of a long cavity in a tree, about ten feet (3 m) below the comb of a monoceros colony'. He concludes that 'it is most probable that this mass represented an accumulation of lichen balls which had been accidentally dropped from the nest above, rather than an intentional store of food'.

**Place of the parent couple and their movements.**—One of the main purposes of the excavations of nests near the field laboratory, just related, was to find the parent couple. In the first-mentioned case the breaking up of the comb into small pieces did not reveal them. However, when all the galleries and cavities in the split trunk were searched the female (queen) was finally detected at a place 15 cm above the site of the comb. It was surrounded by a crowd of workers (was 'evacuated by the workers' as the reporter expressed it). No cell was found.

The rather short note left about the investigation of the second nest on 8.12.1940 shows that a well-defined and thick walled parent cell was found in the centre of the comb and this is mentioned as the place where the male parent was met with. The female was not discovered. This finding will be discussed presently.

The more detailed note on the investigation of the third nest (9.3.1941) describes how the male was found moving on the soil covering the top of the comb after the excavation and lifting. Afterwards the female was traced in the lower part of the comb. Both were surrounded by a crowd of workers. It was emphasized that no parent cell was discovered in the comb when this was broken up.

In the fourth nest (opened on 14.5.1941) examination of the comb after its removal and breaking up did not reveal the parent couple. The stump was then split and knocked with a heavy tool. This produced a lot of eggs and young brood, and then the female was found squeezed in a narrow passage. Later on the male was also found, it had been hit by the tool and was lying on the ground in the midst of the brood. Again a parent cell did not occur in the comb.

BLIJNDORP (1941) giving details on the inner structure of *H. diurnus* habitations which are apparently based mainly on the same reports as I have used here, states that a royal cell is to be found high up in the nests, built apparently of the same material as the rest of the nest. His additional description of the cell and the picture he gives of its outward appearance

and a cross cut show a thick walled clump which is similar to that of royal cells of the subterranean termites, except in one respect. In the bottom a single opening was found "of much greater width than all the others and (is) connected with a system of abnormally wide galleries, which enables the queen to leave her cell". That each *diurnus* nest has a royal cell like this is not confirmed by the reports of the personnel of the field laboratory, nor has a similar cell been met with either in nests of other *Hospitalitermes* species or in those of the related genus *Lacessititermes*, investigated by other workers. Moreover the site of the parent couple in nests of Nasutitermitinae appears to be found, as a rule, in some central or almost inaccessible part of the main comb. This place may have thicker walls or partitions but does not take the shape of a lump, which can be broken loose from the rest of the comb. Therefore we must assume that colony nr 2 has made use of a former nest site or cavity of a Macrotermitine or related species. The situation in the three other nests, which did not show any indication of the presence of a parent cell, may in my opinion be considered the normal one.

BLIJNDORP stresses the point that the queen of the *H. diurnus* colonies is able to flee from its hiding place if the nest is disturbed. 'On her flight she is surrounded by a lifeguard of workers lifting and pushing her swollen abdomen.' This is mainly in corroboration of communications by BUGNION (1909) and JOHN (1913) concerning *H. monoceros*. The first author writes that the queen is capable of some movement of its own 'marchant à petits pas de côté et d'autre'. The second author observed the ability of the parent female to move horizontally at a comparatively rapid pace without aid and to crawl up a vertical post for a foot or so aided by workers pushing her up.

#### ***Observations on H. ferrugineus and H. umbrinus sharpi.***

Very little new information can be given about these species. JOHN described *ferrugineus* from specimens taken from a marching column in the lowland jungle of Siak, E. Sumatra. He did not succeed in finding the nest. Two samples of the species (det. HARRIS) were collected by a Javanese assistant in the mixed forests in the plain near Pemalang, forest district Bantarbolang, North Coast of C. Java. The collector called it 'sumpyoh item' (= black sympyoh), thus distinguishing it from "sumpyoh merah tua" (dark red s.), *H. diurnus*, which was met with in the same locality. This colour indication appears to be in contradiction with the description given by JOHN. One of the samples was taken from a column moving along a felled trunk (9.6.1928), the other from a nest in a large crevice in a standing tree of *Homalium tomentosum*, the cleft extending from 0.5 m at the base up to 4 m. The latter sample contained nymphs. (See last paragraph for the presence of snake eggs in this nest.) The nest reproduced in plate C, 4 was found by the writer in



the company of the adjunct forest entomologist F. A. Th. H. VERBEEK in the same forest district in July 1931. Again the colony lived in a large cavity in the living trunk of a big tree, this time probably a *Ficus*.

*H. umbrinus sharpi* was observed by me at least four times (1931-1935) in the forest complex near Banjar, W. Java, where parts of the original heavy jungle were being converted into teak plantations. Its columns were seen traversing a stony path and descending the exposed roots of a tree (Plate A, 1, 2). A very dense group laden with their little balls of collected material and halting at the base of a big tree on their return to the nest at noon, was also photographed (Plate A, b). Another sample was collected from a stream ascending a teak tree comprising individuals laden with their forage, at 8.30 in the morning. A nest was detected by a pile of black pellets which had accumulated at the base of a large teak tree. The trunk had a hole at 4 m high from which a crust of faecal matter was protruding and which harboured the colony.

**Nesting places of « *Hospitalitermes* » in Sumatra.**—During a visit to clove tree plantations near Manna (on the south west coast of Sumatra) streams of *Hospitalitermes* were seen moving from holes and fissures in the living trunks, three times. In one instance the termite column coming from a hole marched along the interlaced branches of the trees and entered a hole in another trunk.—The holes in these trees were mainly the result of the activities of a moderately large longicorn, *Nothopeus fasciatiipennis* (KALSHOVEN 1950: 717). It may be assumed that the black termites found sufficient room in the long and narrow burrows left by the borer to build their nest. The observations of PETCH have shown that *H. monoceros* can have greatly elongated combs in narrow cavities in tree trunks.—In the nest of *H. medioflavus* described by JACOBSON the comb may well have been hidden in crevices of the rock wall.

In Manna *Hospitalitermes* was also found to be one of three different termite species inhabiting a hole in the base of a large *Ficus* tree. A *Capritermes* colony and a *Rhinotermes* colony occupied the easily accessible outer parts, while the stream of *Hospitalitermes* vanished into a deeper hole. The entrance- (and exit-) galleries of the latter species were situated in the same parts and material as used by the *Capritermes*.

In July 1934 a sample was received of termites from a nest in the base of a 'trentang' tree (*Camposperma* sp.) standing in a felling area on the Isle of Benkalis (along the coast of S. E. Sumatra), where it had been collected by a junior forest officer, ZAMUDIN. The sample was composed of three species, a *Termes* sp. (*Mirotermes*), a small brown *Nasutitermes* and a *Hospitalitermes*. The black termites had been seen inside as well as outside the nest.

In both of these cases we have new examples of compound nest sites as described by JOHN (1925).

***Relations between Hospitalitermes spp. and other animals.***

*Predators.*—No observations are available on predatory ants trying to attack the columns of *H. diurnus* in Java in the manner recorded for *H. monoceros* in Ceylon. However, it has struck me more than once that domestic hens did not peck at the termites in the columns moving about the yard of the field laboratory. Apparently the black termites are in some way objectionable or unpalatable to them, quite in contrast to the common ground-termites like *Macrotermes* and *Microtermes*. It may be assumed therefore that the symphyoh termites are also left alone by the wild fowl in the teak forests including *Gallus varius*, the peacock and the pungklor (*Eucychla*) which are known to feed on termites and can even be raised on them in captivity.

Nothing is known, furthermore, about the attitude of the scaly anteater, *Manis javanica*, a reputed predator of termites, towards the sumpyoh columns. It must be impossible for this animal, at any rate, to reach the nest proper when it is located in narrow cavities.

NIETNER's early note (in HAGEN, 1860, p. 78) mentions a predatory fly which was attracted to opened nests of *H. monoceros* in Ceylon. This may well have been *Ochromyia* (*Bengalia*) *jejuna*, the common robber fly which so ably snatches the brood carried by ant workers and occasionally attacks winged termites too (GREEN in POULTON, 1906). Our notes on *H. diurnus* do not mention the appearance of the Indonesian representative of the genus, *Bengalia latro*, near regularly moving columns or even opened nests of the sumpyoh. It has frequently been observed, however, performing its successful hit and run tactics on disturbed nests of ants and, less often, on opened nests of common ground termites (KALSHOVEN, II, 1951: 884).

Generally speaking, it is hardly conceivable that the black termites could move so freely in the forests as they appear to do, if they were successfully preyed upon by the many insectivorous animals inhabiting the soil and hollow trees, several of which are so keen on other termites. One of the reasons of their relatively little vulnerability must certainly be the efficacious method of defense of the nasuti.

*Termitophils.*—Few observations can be found in the literature about the occurrence of truly termitophilous animals in the nests of *Hospitalitermes* species and little can be added here.

The Javanese assistant who collected the sample of *H. ferrugineus* from the nest in the large crevice of a *Homalium* tree, reported he had found two eggs of a snake in the nest. This reminds one of the occasional presence of snake eggs (*Boiga* sp.) in the globular arboreal nests of *Lacessititermes batavus* Kemn., another day-foraging termite, where eggs occur right in the centre of the comb. Details on three of such findings have been recorded by KOPSTEIN (1935) from W. Java and a fourth case is mentioned in a report on an excursion to a remote locality

in the province of Bantam, W. Java, by VAN DER PIJL (1929). No convincing explanation has been given, so far, of the advantage the snakes might derive from their curious habit of depositing their eggs.

JOHN (1912) has found two specimens of the Cetonid, *Clinteria imperialis* in one of the four nests of *H. monoceros* he investigated in Ceylon. No other instances have become known of a similar association with this or other *Hospitalitermes* species. But typical Cetonid pupal cells, probably of a *Protaetia* sp., have been detected twice in the nest material of an arboreal *Nasutitermes* in Java (KALSHOVEN, 1931; VAN DER PIJL, 1933).

An interesting case of what might be listed under 'termitariophily' was brought to light by JACOBSON. Submitting his material of *H. medioflavus* from W. Sumatra to KEMNER, he included a piece of the outer part of the nest, adding the explanation that the small holes to be seen in the surface were due to the larvae of a certain small beetle which had lived therein (fig. 19, in KEMNER, 1930). Later on he gave a few further details in a note in the journal *De Tropische Natuur* (1933). Here he stated that innumerable larvae lived in the rather hard substance of the nest, tunneling through it in all directions. The beetle reared from it had been identified as *Ptinus rugosithorax* Pic., by ARROW, London. JACOBSON further wrote that the Ptinid larvae were preyed upon by a Clerid. I have found this species was described by CORPORAAL (1939) as *Thaneroclerus termiticola*. Some 600 specimens of the glossy black Ptinid beetle, 2.5 mm in length, all neatly mounted on cards are still present in the collection of the Zoological Museum, Amsterdam.

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# A MORPHOLOGICAL STUDY OF LARVAL DEVELOPMENT IN POLYMORPHIC ALL-WORKER BROODS OF THE ARMY ANT *ECITON BURCHELLI* (1, 2)

by

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## INTRODUCTION

The social behavior of the army ants *Eciton burchelli* and *Eciton hamatum* characterized by alternating, cyclic phases of nomadic and statary activity, is directly dependent upon and synchronized with the development and reproduction of successive all-worker broods appearing at regular intervals (SCHNEIRLA, 1938, 1944 a, 1944 b and 1949). Schneirla's studies show that the larval stage of development of these holometabolous insects occurs in the nomadic phase of activity, and that this phase ends when the mature larvae spin cocoons. In the statary phase which follows, this same developing brood, now enclosed in cocoons, undergoes its pupal period of metamorphosis. Midway through each statary phase, the single queen of each *Eciton* colony lays many thousands of eggs over a period of about six days (SCHNEIRLA, 1953 a). Hence, the embryonic and early larval development of the next brood of ants occurs at the same time that the previous brood is undergoing late pupal development. The statary phase ends when the new adults (or callows) emerge from their cocoons, thus initiating another nomadic phase of activity.

This intricately synchronized life cycle, and its complex behavioral aberrations, continues throughout the year, resulting in the production of polymorphic, all-worker populations ranging near 120,000 individuals every thirty-six days in *burchelli*, and about half as many in *hamatum*. Once a year, at the onset of the dry season, a sexual brood of approximately 1,500 males and about six queen-type females are produced (SCHNEIRLA, 1953 a).

Until SCHNEIRLA's studies, little of the present evidence on the behavior pattern and nothing of the life cycle of these interesting ants were known. Through his work, preserved specimens of their various developmental stages first became available for study, for along with observations on colony behavior of all colonies studied in the field, SCHNEIRLA collected and preserved samples of the adult and developing brood populations. These samples were made available for the present morphological investigations of *Eciton burchelli* and *Eciton hamatum* development.

A review of the literature shows that previous studies of *E. burchelli* all-worker brood development are lacking. Even the most general descriptions of the external morphology of the larvae at any stage are scarce and incomplete. The worker larvae of *E. burchelli* were first described by EMERY (1899 and 1901) and G. C. WHEELER (1943) has added further details to this description. The external morphology of *E. hamatum* worker larvae was described in a preliminary manner by G. C. WHEELER (1938 and 1943) and a more detailed account of this form is reported by TAFURI (1951). Using specimens collected by SCHNEIRLA, TAFURI investigated the developmental morphology of *hamatum* worker larvae with an account of the growth of these polymorphic forms expressed as a ratio of body length to imaginal leg-disc size at successive stages. Also a description of some of the internal anatomy of *hamatum* larvae throughout development is given.

The present investigation was undertaken to study the external and internal morphology of *E. burchelli* throughout most of the stages of larval development to its conclusion, and to determine whether differences in developmental growth rate and in structure exist among the various polymorphic forms of the larval brood. It was found that in the various polymorphic size-groups of *burchelli* larva there are differences in the size and growth rate of the imaginal leg discs throughout development, as well as differences in terms of the 'phase-day' age at which developmental changes in the leg discs and in the labial or spinning glands occur. The times at which such changes are first observed in larvae of the different polymorphic size-groups are correlated with changes in colony behavior and function reported from field studies on this species, and appear to depend upon certain factors underlying differential growth and development of these ants. The present paper is therefore devoted to the description of the external and internal anatomy of *Eciton burchelli* larvae, with emphasis on the developmental morphology of the leg discs and the labial glands.



## MATERIALS AND METHODS

**THE BROOD SAMPLES.**—The *E. burchelli* larvae studied were from the collections of colony samples of the American Museum of Natural History. These samples were collected and preserved by T. C. SCHNEIRLA and R. Z. BROWN on Barro Colorado Island, Canal Zone, Panama, during various field expeditions. The age of the larvae was initially designated upon the basis of specific characteristics noted in colony behavior at the time of collections. All larvae were fixed in Bouin's fixative or 95 per cent alcohol at the time of collection and then stored in 70 per cent alcohol containing two per cent glycerine.

Each day's sample consists of all individuals captured from an all-worker larval brood and preserved on a given day of the statary or nomadic phase. The samples were collected by a procedure intended to give the best obtainable representation of the polymorphic brood range. Because the bivouacs of *burchelli* colonies are at times unapproachable for the collection of any brood sample at all, or may be so situated in the bivouac that the collection of the brood sample is limited to one part of the polymorphic range, no colony in this study is represented by samples at regular intervals throughout development. Therefore, the broad interval from late embryonic to mature larval development had to be represented by samples from different colonies, and thus forms a 'synthetic series' of all-worker *burchelli* brood development. The samples studied, which collectively represent *burchelli* brood development were: '52 B-Is, last statary day; '47 B-II, third, eighth and tenth nomadic days; '46 B-IV, fifth and seventh nomadic days; and '46 B-I, twelfth nomadic day. Additional studies of *burchelli* larvae were carried out on samples of '53 B-II, third nomadic day; '53 B-I, ninth nomadic day; and '46 B-I, last nomadic day.

Each colony number designates the particular colony on which detailed field observations of colony behavior were made by SCHNEIRLA (SCHNEIRLA, 1949, and SCHNEIRLA and BROWN, 1952). For example, '46 B-IV signifies the fourth *E. burchelli* colony studied in 1946.

Since at each successive time throughout the activity cycle of the terrestrial Ecitons, characteristic changes are noted in the developmental condition of the brood (SCHNEIRLA, 1934, 1944 b and 1953 a; SCHNEIRLA and BROWN, 1950), each further day's sample may be considered to represent an advance in development. This correspondence has been found to hold in all colonies. However, in the present study of the synthetic series assembled from different colonies for the study of all-worker brood development of *burchelli*, secondary variants appear which may modify, to a limited extent, the relationship of the 'phase-day' age to the developmental stage which would be expected in the brood of a single colony. These may be the results not only of limited inter-colony differences, but also of deviations in the intervals due to the impossibility of collecting the samples at the same time of day.

**SELECTION OF SPECIMENS IN THE POLYMORPHIC RANGE.**—The number of *burchelli* larvae in each day's sample varied from approximately 150 to 3,000-4,000, with the usual number about 300-400. To insure a study of the complete range of polymorphic larval forms present in each sample, eight of the largest specimens, eight of the smallest and 24 of sizes graded between the extremes were selected to represent each sample. A dissecting microscope was used in selecting specimens of the early developmental stages. Half of these larvae (four large, four small and twelve of graded sizes) thus taken from each day's sample were measured in detail and a study was made of their external and internal morphology. The remaining 20 were used for dissections and for whole mount preparations.

**STUDY OF EXTERNAL AND INTERNAL MORPHOLOGY.**—The *burchelli* larvae selected for study of their external morphology were examined under a dissection microscope and the following data were recorded: The shape of the larva and its state of preservation; the condition of the cuticle; the presence, quantity and distribution of cuticular hairs; the transparency of the cuticle; the presence and extent of development of the imaginal

leg discs (their size, shape, segmentation and position with respect to the margin of their segment); and the presence and state of development of the antennal discs, the gonopodal discs and the mouth parts. Measurements were taken of the total body length and width and the dimensions of various segments, also the length and width of one randomly selected left or right leg disc of each of the three pairs.

All of the measurements were made with a filar micrometer except in the case of total body length, for which an ocular micrometer was used.

For study of the internal morphology of *burchelli* larvae the specimens were dehydrated and imbedded in paraffin using the normal butyl alcohol method (LEE, 1937). Sections were cut at six micra and stained with either Heidenhain's iron alum haematoxylin or Harris' standard haematoxylin counterstained with eosin (GALIGHER, 1934). Whole mounts of the larvae, and of dissected organs, were prepared using Lynch's precipitated borax-carmin technique (GALIGHER, 1934).

## RESULTS

### EXTERNAL MORPHOLOGY

*General inspection of the polymorphic larval range.*—It is apparent from the results of this study that the larvae in the sample of any one day are not synchronized linearly, and that they must differ either in the time at which their respective larval developments were initiated, in the rate of their development, or in both of these. This impression is soon borne out by the results of general body measurements as of length in relation to specific measurements of body parts such as leg discs (table 1).

First, an inspection of the brood sample collected at any one time reveals a wide range in body length with indications of individual differences in detailed morphology possibly bearing a different relationship to overall body size in the respective parts of the range. That this must be the case becomes evident when individual differences in the degree of development of detailed larval structures such as the leg discs, mouth parts, cuticular hairs and the gonopodal discs are taken into account. The general picture indicated is one in which, at any one cross-section in time, a smooth gradation is found from specimens of maximal to those of minimal body length, with differences in the time of appearance, size, and degree of development of structural details relative to differences in overall size.

Furthermore, when specimens from samples collected at successive different times are compared, it is apparent that overall size cannot be a reliable clue to developmental stage, unless the relationship between body size and the condition of the details of structures is taken into account.

*The largest larvae or potential workers major.*—The largest larval specimens, apparently the potential workers major, evidently develop from the first eggs to hatch and thus obtain a precocious growth advantage over the smaller members which hatch from their eggs in the late statary

AGE	GROUP**	BODY LENGTH IN mm.			AREA LEG DISCS IN mm <sup>2</sup>			RATIO*** IN LOG 10 <sup>-4</sup>
		RANGE			RANGE			
		MINIMUM	MAXIMUM	AVERAGE	MINIMUM	MAXIMUM	AVERAGE	
LAST STATARY DAY	S	0.504	0.604	0.513	.000	.000	.000	0
	G	0.717	2.076	1.248	.000	.000	.000	0
	L	2.604	2.982	2.651	.004	.006	.005	1.276
3rd NOMADIC DAY	S	0.520	0.569	0.548	.000	.000	.000	0
	G	0.604	3.434	1.544	.000	.008	.001	0.811
	L	4.189	5.887	4.651	.001	.013	.008	1.236
5th NOMADIC DAY	S	1.510	1.698	1.528	.000	.003	.000	0
	G	1.736	5.623	3.658	.000	.020	.005	1.135
	L	5.623	7.322	6.095	.011	.030	.011	1.255
7th NOMADIC DAY	S	1.925	4.604	3.201	.000	.012	.000	0
	G	4.944	7.472	6.091	.000	.037	.006	0.993
	L	7.661	8.739	7.557	.000	.019	.003	0.598
8th NOMADIC DAY	S	0.906	1.547	1.246	.000	.000	.000	0
	G	2.717	6.302	4.013	.000	.022	.010	1.396
	L	6.680	9.107	7.086	.000	.029	.022	1.492
10th NOMADIC DAY	S	2.076	3.107	2.726	.000	.007	.001	0.564
	G	3.623	7.548	5.642	.000	.054	.023	1.610
	L	8.152	10.000	8.095	.000	.066	.038	1.666
11th NOMADIC DAY	S	4.416	5.170	4.838	.012	.016	.013	1.429
	G	5.812	8.000	6.391	.016	.048	.027	1.626
	L	9.095	10.492	9.086	.013	.049	.032	1.547
12th NOMADIC DAY	S	3.700	4.868	4.112	.009	.022	.017	1.616
	G	5.170	9.360	6.866	.000	.050	.024	1.543
	L	9.624	13.800	11.405	.000	.088	.022	1.285

\* The four smallest individuals are grouped under letter S, the four largest individuals are grouped under letter L, and the twelve individuals of graded sizes are grouped under letter G.

\*\* The ratio here listed was obtained by dividing the average leg discs' area by the average body length.

TABLE 1. — Measurements of *Eciton burcheelli* larvae throughout development.

or early nomadic phase. This precocious growth advantage is maintained throughout the entire larval stage of development. Thus, in samples taken at the earliest larval stages, prominent morphological features such as the earliest stages of development of the mouth parts, the imaginal leg discs, the antennal and gonopodal discs and the cuticular hairs are observed in the specimens having the greatest body length and width, but not in the smallest larvae. It should be noted then that there are two methods of calibrating developmental progress: First, by using the nomadic day, that is, specimen staken from day one to day thirteen, each day denoting the development in termes of the representative duration of time. A second method of calibrating developmental progress makes use of the developmental stage. Here the different polymorphic types are considered roughly comparable in the time at which hatching occurs, in the representative times thereafter in which corresponding changes appear in structure (e.g., leg discs), and in the respective times at which they attain larval maturity. In general,



as table 2 shows, these corresponding changes appear first in the largest larvae, next in the larvae of intermediate sizes and last in the smallest larvae.

TIME OF APPEARANCE OF DEVELOPMENTAL CHARACTERISTICS OF AN ALL-WORKER LARVAL BROOD OF *ECITON BURCHELLI*

LARVAL SIZE	LARGEST (POTENTIAL WORKER MAJORS)	INTERMEDIATE (POTENTIAL WORKER INTERMEDIATES)	SMALLEST (POTENTIAL WORKER MINIMAS)
<u>EXTERNAL DEVELOPMENT</u>			
	TIME OF FIRST APPEARANCE		
EMBRYONIC DEVELOPMENT	MIDDLE TO LATE STATORY PHASE	LATE STATORY PHASE	VERY EARLY NOMADIC PHASE.
CUTICULAR HAIR DEVELOPMENT	LAST STATORY DAY.	3 <sup>RD</sup> TO 5 <sup>TH</sup> NOMADIC DAYS	7 <sup>TH</sup> NOMADIC DAY.
MOUTH PARTS DEVELOPMENT	LAST STATORY AND FIRST NOMADIC DAYS.	5 <sup>TH</sup> TO 7 <sup>TH</sup> NOMADIC DAYS	11 <sup>TH</sup> TO 13 <sup>TH</sup> NOMADIC DAYS
IMAGINAL LEG-DISC DEVELOPMENT	LAST STATORY DAY	3 <sup>RD</sup> TO 7 <sup>TH</sup> NOMADIC DAYS.	8 <sup>TH</sup> TO 9 <sup>TH</sup> NOMADIC DAYS
<u>INTERNAL DEVELOPMENT</u>			
	FUNCTIONAL ONSET OF SALIVARY SECRETION		
BASOPHILIC PROLIFERATION OF GLANDULAR PORTION	LAST STATORY AND FIRST NOMADIC DAYS.	3 <sup>RD</sup> NOMADIC DAY	MAINLY BY 6 <sup>TH</sup> NOMADIC DAY.
LABIAL PORTION DENSE CYTOPLASM, AND IRREGULARITY OF CUBOIDAL CELLS.	8 <sup>TH</sup> NOMADIC DAY.	9 <sup>TH</sup> NOMADIC DAY	10 <sup>TH</sup> NOMADIC DAY
ANTERIOR DUCT AND GLANDULAR PORTIONS DISINTEGRATING.	10 <sup>TH</sup> NOMADIC DAY	11 <sup>TH</sup> NOMADIC DAY	12 <sup>TH</sup> AND LAST NOMADIC DAYS
ACCUMULATION OF ACIDOPHILIC MATERIAL IN LUMEN	10 <sup>TH</sup> NOMADIC DAY.	12 <sup>TH</sup> AND LAST NOMADIC DAYS	13 <sup>TH</sup> NOMADIC DAY

TABLE 2. — The times of first appearance and of the apparent onset of function of various external and internal structures and various organs characteristic throughout development in all-worker larval broods of *Eciton burchelli*.

A precocious growth in the largest larvae is indicated by the fact that in the material studied, the largest members of the sample taken at the tenth nomadic day may be considered fully mature and ready to enter the prepupal period of metamorphosis at a time when smaller members of the range are relatively less mature. At this time these larvae approximate a cylindrical shape with their narrow anterior ends curved ventrally (fig. 1). The body widens posteriorly to the region of the fourth or fifth abdominal segment, where it begins to taper and finally terminates bluntly at the posterior end. All of the larvae have fourteen segments,—a head segment, three thoracic segments and ten abdominal segments. The last abdominal segment is usually small and not as distinct as the other thirteen.

*Structural indications of development.*

A. **Shape and body curvature.** — During embryonic and early larval development, the head segment is the largest segment of the body, but by the time the larvae reach a length of approximately one millimeter, the

thoracic segments have become the largest segments, and the widest part of the larvae is in the abdominal region.

In preserved larvae representing very early stages (e.g., the last statary and the third nomadic days) the largest larvae show little ventral curvature in their anterior segments, in contrast to the considerable curvature noted in mature specimens (e.g., the largest larvae of the tenth nomadic day and the intermediate specimens of the last nomadic day). It therefore appears that a direct relationship exists between the amount of body curvature and body length in the preserved material. In all the polymorphic forms, just before maturity, the larger the larva the greater the amount of curvature.

**B. Cuticle.**—Although in most of the *burchelli* larvae studied the cuticle was characteristically papillose as described by G. C. WHEELER (1943), a relatively smooth cuticle was observed in many instances. This is probably related to the occurrence of moulting, for when a double cuticle is seen its inner cuticle is invariably papillose, whereas the outer cuticle is usually smooth. In the mature larva the cuticle is opaque in all segments except the head segment where it is slightly transparent, whereas in younger and smaller larvae the cuticle is very transparent so that the nerve cord, digestive tract and other internal organs can be seen through it. As development proceeds, the cuticle becomes opaque and may take on a chalky appearance in various regions.

Study of the appearance of cuticular hairs on the different regions of larvae in the successive samples, and the progressive development of the hirsute covering, revealed that at early stages (e.g., in larvae of the last statary day) the cuticle possesses hairs only in the largest larvae, (e.g., longer than 3.4 mm) and is smooth in larvae of the smaller sizes. This condition persists, substantially as described, in more advanced samples taken on the 3rd., 5th. and 7th. nomadic days. A relative change, i.e., appearance of a hirsute cuticular condition in the smaller castes, is indicated by the fact that minute, bristle-like hairs are present on the head and thorax of the 3.5 to 5.8 mm larvae of the third nomadic day and on the 3.4 to 5.0 mm larvae of the fifth nomadic day. Numerous short, simple hairs are present on the head, thorax and posterior end of the abdomen in the 5.7 to 7.3 mm larvae of the fifth nomadic day, and on all larvae greater than 3.4 mm of the seventh nomadic day. The largest larvae of the seventh nomadic day, and successively smaller individuals of further nomadic days, have progressively more hairs on their thorax and abdomen, another indication that hirsuteness varies in relation to body length and age. In samples taken at the tenth nomadic day, when the largest larvae have reached maturity, all the larvae throughout the range from smallest to largest are covered with numerous hairs quite evenly distributed over the surface of the body.

**C. Mouth parts.**—In the mature larvae, the mouth parts are the dorsally situated fleshy labrum, the dorso-lateral heavily sclerotized, sickle-shaped

mandibles, the large fleshy laterally arranged maxillae, and the ventral labium (figs. 2 and 3). The maxillae possess two pairs of palps; the conically-shaped, sclerotized galea, and the more posteriorly situated maxillary palps (fig. 2). The latter, are broad, roughly ridged and sclerotized. On the anterior surface of the labium, and slightly elevated, is the horizontal, slit-like opening of the labial glands, or sericteries. Just lateral to this opening are the minute, conically-shaped, slightly sclerotized labial palps (figs. 2 and 3).

This description of the mouth parts agrees with the previously reported mouth parts for the larva of *E. burchelli* (EMERY, 1899 and 1901, and G. C. WHEELER, 1943).

The labrum, mandibles, maxillae and labium appear first in the largest (.604 mm) larvae at earliest stages (last statary and third nomadic days), and in all larger and older samples they are found throughout the size range. Throughout the nomadic phase of development the mandibles are heavily sclerotized in larvae of all sizes. The galea and maxillary palps, in contrast, first appear and subsequently become sclerotized at a different time, a fact which is found to serve as an index to larval maturity.

The galea and maxillary palps also develop precociously in the largest larvae, as is indicated by the fact that their most sclerotized condition is observed first in the largest larvae of each successive sample. In the sample of the thirteenth day, in which distinct signs of maturity are noted throughout the larval brood, even the smallest larvae exhibit an advanced degree of development in these structures. Of course, at all stages these structures, and others as well, exhibit size variations related to overall body size.

These studies indicate a developmental precocity which is greatest in the largest larvae, very probably the potential workers major, and least in the smallest larvae, or potential workers minima. However, there are indications that although the smallest larvae are last to complete the initial period of slower overall developmental acceleration, in their case the rate of development of these structures is subsequently greater than in the larger larvae (intermediate and major castes). This point may be better examined with respect to the imaginal leg discs, which make their first appearance at different times and undergo their subsequent growth at a different rate in larvae of the three size groups selected for study.

**D. Imaginal leg discs.**—G. C. WHEELER (1938), in describing the vestigial legs of the army ant larva, has referred to the relevant imaginal discs. These are three pairs of round or oval patches of hypodermis located on the ventral surface of the thoracic segments (fig. 4). The first appearance and progressive enlargement of the imaginal leg discs occur at a different time and at a different rate in larvae of each of the three polymorphic size groups. In our earliest samples (i.e., from the last statary and first nomadic days) the discs are found only in the largest larvae; in subsequent samples they are found successively later in the



intermediate and the smallest larvae. The leg discs were not found in the smallest or minim larvae before the sample of the seventh nomadic day.

**E. Differential growth rate of the leg discs.**—As the imaginal leg discs represent our indicator of local growth in the more detailed study of development in *Eciton burchelli* larvae, it is appropriate here to describe in further detail how the obtained measurements were treated. First, one randomly selected member of each pair of imaginal leg discs was measured in its length and width in each specimen of the four largest, four smallest, and twelve larvae of intervening sizes in each sample, with each of the larvae also measured in its overall body length. Then a theoretical expression was obtained for leg disc status in each larva by first obtaining the *length*  $\times$  *width* product for each of the three discs measured, then averaging, the three products for each individual. These results are listed in Table 1, as three groups of averages of the larval leg-disc areas for each developmental stage studied, together with the similarly averaged ratios obtained by calculating *body length* : *leg-disc area*. This ratio of body length to the leg-disc area value serves as an expression of allometric growth status for larvae in samples taken at different stages of development.

With very few exceptions, primary developmental stages of the imaginal leg discs are present in *burchelli* larvae with body length greater than 2.6 mm of the last statary day; 2.4 mm of the third nomadic day; 2.3 mm of the fifth nomadic day; 2.0 mm of the seventh nomadic day; 2.7 mm of the eighth; 2.9 mm of the tenth and in all individuals of successive nomadic days. Hence there appears to be a relationship between the onset of leg-disc development and the attainment of a given threshold of size in the larva rather than to the phase-day age of the larvae. This is evident when one considers the fact that leg discs appear at correspondingly later phase-day ages in those larvae lest to hatch and to begin their development (i.e., in the smallest or potential minim castes).

In all samples, the leg discs exhibit their most advanced stages in the largest larvae. Thus in the sample of the third nomadic day, the presence of the peripodal cavity is apparent in some of the largest larvae but in none of the smaller specimens. In like manner, in the sample of the fifth nomadic day the presence of transverse segmentation in these discs is apparent in some of the largest larvae but not in any of the smaller specimens. These changes in the development of the leg discs are always observed first in the largest larvae, only later in the intermediate (size-graded) larvae, and last in the smallest larvae. With continued development the leg discs of some of the largest and size-graded larvae of the tenth, eleventh and twelfth nomadic days overlap the posterior margin of their thoracic segment and are partially or entirely covered by the surface integument. Consequently, most of the largest larvae of the twelfth nomadic day have no externally visible imaginal leg discs, so that

zero values for leg discs' areas had to be recorded for some of these larvae (table 1).

A graphic representation of the ratios of leg-disc area to body length is given in figure 5 for different times in larval development in the largest, the size-grade (intermediate) and the smallest polymorphic *burchelli* larvae. Leg-disc measurements of larvae of one sample, that of the seventh nomadic day, were excluded from the final analysis of this relation-

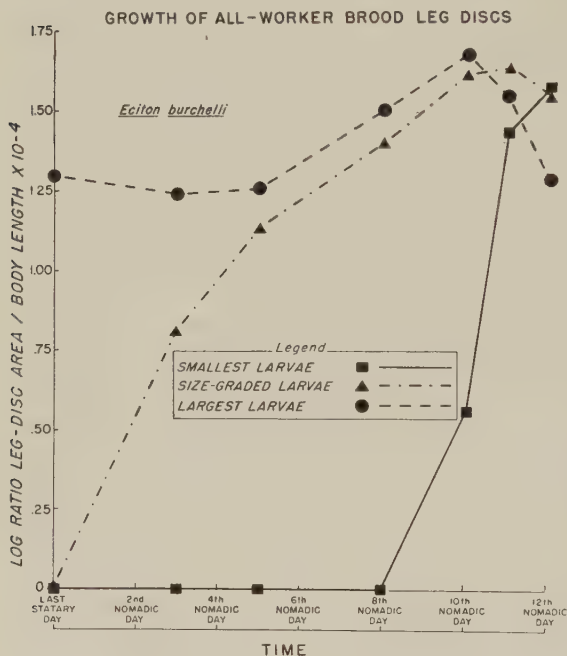


FIG. 5. — Ratio of local and general growth as a function of time throughout larval development in a "synthetic" series representing all-worker broods of *Eciton burchelli*.

last days of the nomadic phase. This last fact is accounted for not only by a proliferation of the leg discs themselves beneath the integument at this stage, but also by a partial overgrowing of the discs by the surface integument.

**F. Other external structures.**—The paired antennal discs are located on the dorso-lateral surface of the head segment (fig. 3). The gonopodal discs, which are paired, and round or oval in shape, are located on the ventral surface of the seventh, eighth and ninth abdominal segments. The discs of the seventh segment are widely spaced on the segment while those on the eighth and ninth segments are situated nearer the midline. Although the antennal and gonopodal discs are relatively small, opaque patches of the hypodermis, in their first appearance and sequence of

ship, since many of these specimens were found noticeably mutilated in the thoracic region. Leg-disc growth rate is indicated by the rate of change in the slope of the line. This graph shows that once leg-disc development is initiated, its growth rate is very different in each of the three groups; it is slowest in the largest larvae, intermediate in the size-graded larvae, and fastest in the smallest larvae. Also shown here is the precocious development of the leg discs in the largest and size-graded larvae during the early and middle days of the nomadic phase, as well as the precocious decrease in leg-disc surface area in these larvae during the

developmental changes throughout larval life, they are closely similar to the imaginal leg discs.

Among other external structures studied in *burchelli* larvae was a holopneustic type of respiratory system which has some of its simple, anastomosing tracheae externally visible through the cuticle. Also in larvae of all sizes, ten pairs of spiracles are present as small, sclerotized, cuticular openings on the dorsolateral surface of the third through twelfth larval segments.

The anal opening is present in all larvae as a transverse slit on the ventral surface of the 14th. segment.

### INTERNAL MORPHOLOGY

General inspection of the polymorphic larval range.—Results from microscopic observations of the internal morphology of larvae through the polymorphic range of any one day's sample do not indicate a linear progression synchronized either in the time of initiation of organ development or in the rate of onset of organ function. With respect to their internal structures, the largest larvae in each day's sample were more advanced in development than were the intermediate (size-graded) or smallest larvae of that sample. In all larvae, the size of the internal organs varies directly with body length, and consequently, a smooth series in the sizes of organs is found between the extremes in body length.

Consideration of all samples throughout development indicates that the onset of activity of the various organs and organ systems is observed first in the largest larvae of each day's sample. However, neither the characteristics of any one internal structure nor of any one tissue could be used to distinguish the various polymorphic forms *per se*.

**A. Alimentary canal.**—The alimentary canal of *burchelli* larvae is essentially a straight tube divided into the foregut, midgut and hindgut (figs. 6, 7, 8, 9, 10, 11 and 12). The foregut extends from its anterior limit at the mouth opening to the region of the metathoracic segment. It proceeds posteriorly as a narrow tube and then reflects upon itself in the prothoracic segment to form the esophageal invagination or cardiac valve. This valve projects into the lumen of the midgut. The foregut is composed of the buccal cavity, the pharynx, the esophagus and the reflected portion of the esophagus, the cardiac valve. The cardiac valve terminates the foregut in the metathoracic segment (fig. 8).

The midgut extends from the mesothoracic segment to the eleventh segment as a large, dilated, blind sac. The midgut is the largest organ of the larva and appears to serve as a mould around which the other abdominal organs are oriented (fig. 6).

The hindgut extends from the blind, posterior limit of the midgut to the ventral surface of the fourteenth segment where it opens to the exterior



at the anal opening. The hindgut is composed of a short, narrow intestine, the expanded rectum and a constricted posterior end, the anus (fig. 9). The four Malpighian tubules are attached to the most anterior portion of the intestine in the region of the twelfth larval segment. The lumina of the mid and hindguts are not continuous until late in the prepupal or early pupal period of metamorphosis.

Once the foregut is established early in larval development, its morphology remains virtually unchanged throughout larval development. In contrast, the midgut appears to be continually changing in its cytological make-up during late embryonic stages, and throughout larval development. The blind, sac-like midgut epithelium is composed of a single layer of extremely large, flat, polygonal-shaped cells (figs. 8 and 11). Early in larval development these cells have distinct round or oval nuclei surrounded by dense, granular cytoplasm. With age, these nuclei become amoeboid in outline and cytoplasmic changes are evident which result in the histolysis of these cells.

In early stages the hindgut is a relatively narrow tube with columnar-shaped epithelial cells, but with further development, the various regions of the hindgut become differentiated (fig. 9). In some of the large larvae of the fifth nomadic day, as well as in the intermediate and smallest larvae of the seventh and all further nomadic days, the hindgut is fully differentiated into intestine, rectum and anal portions. In larvae of all sizes, in the last stages of larval development, the rectum appears to be contracted, and crystalline material, previously observed in the expanded rectal portion of younger larvae, is now evident in the anal portion of the hindgut.

**B. Malpighian tubules.**—In larvae of all sizes, and at all stages of development, the four Malpighian tubules are symmetrically arranged along the dorsolateral and ventrolateral sides of the midgut as two pairs of straight, narrow tubes. These tubes extend anteriorly from their point of attachment on the anterior, dorso-lateral part of the intestine in the twelfth segment, to the region of the fifth or sixth segment and have a rather uniform diameter throughout. The blind, free ends of these tubules are slightly curved, but in the posterior attached region the two ventral tubules are intimately associated with the anteriorly directed branches of the glandular portion of the labial glands.

The Malpighian tubules are composed of a single layer of epithelial cells, roughly cuboidal in shape, which have distinct, ovoid nuclei surrounded by an irregular, fibrillar arrangement of cytoplasm. The inner, free surfaces of these cells are distinctly convex in the largest larvae of the last statary and third nomadic days, as well as in all larvae of further nomadic days (figs. 13, 14 and 15). However, in the smallest and intermediate larvae of the last statary and third nomadic days these cells are more cuboidal in shape.

Throughout larval development the cells of the Malpighian tubules increase in size and show cytoplasmic variations indicative of the functional activity of this organ. With further differentiation, these nuclei

become amoeboid in outline and histolysis of the larval Malpighian tubules is observed only in those larva which have become enclosed in cocoons (i.e. are in the prepupal period of metamorphosis).

In the large larvae of the ninth and tenth nomadic days, the anlagen of the adult Malpighian tubules are arranged in a small cluster around the larval intestine just posterior to the point of attachment of the larval Malpighian tubules (fig. 15).

**C. The nervous system.**—The larval nervous system of *Eciton burchelli* is composed of the central and the stomatogastric nervous systems. The central nervous system consists of the *supra-esophageal ganglion* or *brain*, and a series of twelve, ventrally located, paired *ganglia* of the nerve cord with their respective nerves (figs. 6 and 12). The *stomatogastric nervous system* consists mainly of a median, bean-shaped, frontal ganglion with its anterior bilateral and posterior median nerves (fig. 12).

The *brain*, a pair of large, roughly egg-shaped ganglia, is located in the head segment. These ganglia are almost completely separated medially by a deep, antero-posterior sulcus, across which they are held together by connecting nerve fibre tracts. This *median commissure* is located in the posterior part of the brain just dorsal to the esophagus. At the anterior, ventral region of the brain, three pairs of nerves are evident. The most anterior pair extend to the region of the labium; the middle pair serves as a ventral, interlobular commissure and lies just ventral to the pharynx (fig. 10). The posterior pair extends ventrally and forms the circum-esophageal connectives which join together the supra-esophageal and sub-esophageal ganglia. The ventral interlobular commissure together with the dorsal interlobular commissure form the *circumpharyngeal nerve ring* through which pass the pharynx and esophagus.

The first ganglion of the ventral nerve cord is the *sub-esophageal ganglion*, located ventrally between the head and prothoracic segments (figs. 6, 7, 16 and 17). This ganglion is connected with the second ventral ganglion of the nerve cord, the prothoracic ganglion, by two longitudinal connectives. All successive ventral ganglia are connected similarly, forming a *ventral nerve cord* which has a morphological pattern typical of insect larvae. In the twelfth segment, the last ventral ganglion is relatively large and the nerve tracts within this ganglion unite to form a single, terminal nerve. This nerve projects into the haemocoel of the posterior region of the larvae and branches of it may be clearly seen to reach the rectum and hindgut.

The brain and ventral ganglia are composed of neuroblasts and fibrous tracts. In larvae of early stages, the neuroblasts, which are actively dividing, basophilic-staining cells with dense, ovoid nuclei, are more prevalent than the fibrous tracts (fig. 6). As the larva approach maturity, the abundance of nerve tracts within the nervous system becomes more evident. In the last stages of larval development the brain lobes and ventral nerve cord are highly differentiated into central regions of nerve

tracts and cortical regions of nerve cells (figs. 7 and 10). Throughout development the central nervous system is covered by a nucleated membrane, the neurilemma (figs. 10, 12 and 16).

In all larvae the brain is the most prominent internal organ of the head segment, and its size increases throughout development. In the large larvae of the eighth nomadic day, and in larvae of successive nomadic days, the lobes of the brain extend slightly into the prothoracic segment.

The *frontal ganglion* of the stomatogastric nervous system is located dorsal to the pharynx, just below and in front of the brain lobes. This bean-shaped ganglion has a central core composed of tracts which are surrounded by neuroblasts (fig. 12). Fibers extend bilaterally from the anterior limit of this ganglion, while a single, relatively large, posteriorly directed nerve, the *recurrent nerve*, extends from its posterior limit (fig. 10, 12 and 16). This nerve passes dorsal to the foregut, and many of its branches clearly reach the pharynx, the oesophagus and the oesophageal invagination; *i.e.*, the cardiac valve.

**D. The secretory system.**—1. THE CORPORA ALLATA.—The *corpora allata*, a pair of endocrine glands which from developmental studies of other insects are believed to be associated functionally with the stomatogastric nervous system, are distinctly present in all individuals of the polymorphic series of *burchelli* larvae. In all stages of larval development they are oval, compact lobes of spherical cells, located on either side of the foregut and just posterior to the circumpharyngeal nerve ring (fig. 16). These cells are differentiated into a central core of densely basophilic-staining cells surrounded by a slightly less dense, basophilic-staining peripheral region. The cells of both regions have distinct ovoid nuclei surrounded by granular cytoplasm.

The corpora allata are surrounded by a network of tracheoles and are suspended in the blood sinuses by these tracheoles and nerves of the central and stomatogastric nervous systems. In the materials studied, in larvae of the different polymorphic size groups, the corpora allata were distinguishable only in size, which in all cases seems to be directly proportional to the overall size of the individual larva.

2) THE LABIAL GLANDS.—Throughout the course of larval development in the worker broods of *Eciton burchelli*, a series of significant morphological and histological changes of the labial glands is apparent. These changes evidently result in the two-fold functional activity of this gland; first, as the site of production of the labial secretion, and second, as the site of production and accumulation of the precursor of the spinning silk. Histological signs of the onset of activity of the labial glands, and of their subsequent change in function, are always observed first in the largest polymorphic size larvae, second in the intermediate larvae, and last in the smallest larvae. The 'phase-day' age at which the functional activity of these glands begins evidently is one of the factors underlying differential



growth and development among larvae of the different polymorphic groups and is believed by SCHNEIRLA to be related to the amount of stimulative and trophic exchange between adults and brood resulting in varied levels of colony excitation.

The labial glands of mature *burchelli* larvae are bilaterally arranged, branched, tubular structures which lie ventral and lateral to the alimentary canal, and open on the labium. They are divided into the duct portion, the saccus portion, and the glandular portion, and extend from the labium to the eleventh or twelfth larval segment. These glands are the sericteries or spinning glands of the larva, and the terminology adopted here for their various portions is in agreement with that previously used for *Myrmica schencki* by STÄRKE (1948) and for *Eciton hamatum* by TAFURI (1951).

The duct portion of this gland is divided into the common duct of the labial gland and the paired branches of this duct, the ducts of the labial gland. The common duct extends from the opening on the labium to the prothoracic segment, where the ducts of the labial gland are also located. Each saccus portion extends from the posterior region of the prothoracic segment to the fifth or sixth segment; each glandular portion extends from this region to the tenth or eleventh segment where it branches dichotomously. One branch extends posteriorly to the twelfth segment where it terminates as a blind tube; the other turns dorsally and proceeds anteriorly to the region of the seventh or eighth segment, where it too terminates blindly.

In mature larvae of all the polymorphic size groups the three portions of the labial glands differ histologically although the entire gland is composed of simple epithelium arranged on a distinct basement membrane. During early larval development, however, the saccus and glandular portions are nearly identical and are composed of simple, cuboidal shaped cells. The lumina of the saccus and glandular portions at this time are extremely narrow and of uniform diameter (figs. 13 and 18). The duct portion is composed of high cuboidal-shaped cells which surround a distinct lumen (fig. 18). This early stage of labial gland development is found in all the smallest and in some of the intermediate larvae of the last statary day, and in some of the smallest larvae of the third and fifth nomadic day's samples.

In the largest and some of the intermediate size larvae of the last statary day, and in some of the larger of the intermediate and smallest larvae of the third and fifth nomadic days, the lumen widens at the posterior end of the glandular portion of the labial gland and the cells surrounding it appear larger than in larvae of the respective types at earlier stages. These cells are rather vacuolate at their outer, attached border, and the lumen they surround contains small amounts of a fine, basophilic-staining, granular secretion (fig. 19). The cells of the saccus portion at this time are gradually becoming flatter to assume a low, polygonal shape (fig. 17). Small amounts of the secretory material are

observed in the lumina of the saccus and ducts of the gland at this time, indicating the onset of secretory activity of these labial glands.

An increased secretory activity of the cells of the glandular portion occurs with development. The cells appear more vacuolate at their outer, attached borders while at their inner, free borders the presence of secretory material is evident (fig. 20). The cells of the saccus portion, now squamous in shape, have a uniformly granular cytoplasm. This condition is observed first in the labial glands of some of the largest larvae of the third nomadic day, in the intermediate and smallest larvae of the fifth nomadic day, and occasionally as late as in the smallest larva of the tenth nomadic day.

The height of secretory activity of the labial gland is marked by an increase in the amount of fine, basophilic-staining, secretory material in the lumina of the glandular, saccus and duct portions (figs. 7 and 21). This condition, observed first in some of the largest larvae of the fifth nomadic day, next in the size-graded larvae of the seventh nomadic day and last in some of the smallest larvae of the eighth and tenth nomadic days, is found in all older and more advanced individuals of the respective groups. It persists until the function of this gland changes from the production of the labial secretion to the production of the precursor of the spinning material. This change in function of the labial gland from its primary to its secondary role is noted first in some of the largest larvae of the eighth nomadic day, and next in the largest, the intermediate and some of the smallest larvae of the tenth and eleventh nomadic days. At this time the cells of the glandular portion become enlarged, irregular in shape and stain intensely basophilic (fig. 14). At the correspondingly different times noted above, the lumen of this region becomes almost completely obliterated.

Somewhat later than the last noted time, a fibrous-appearing acidophilic substance begins to accumulate in the lumen of the glandular portion. This is observed in some of the largest larvae of the tenth nomadic day, and in the intermediate and smallest larvae of the eleventh and last nomadic days. This substance, believed to be the precursor of the spinning silk, accumulates first at the terminal ends of the glandular portion and then more anteriorly. The cells surrounding this fibrous material are now low, cuboidal-shaped, deeply staining basophilic cells which have a dense granular cytoplasm (fig. 15). At this stage of labial gland development, the cells of the saccus portion show signs of a cellular breakdown and irregular, coarse, basophilic-staining masses become evident in the lumina of the saccus and ducts (fig. 22 and 23).

To summarize the developmental history and functional activity of the labial glands, corresponding changes in the formation of products of the labial gland occurs in the three arbitrary polymorphic groups at respectively different times in the nomadic phase. At the last statary and early nomadic days only the largest larvae have glands producing salivary secretion. As the nomadic phase proceeds, the size-graded and the smallest larvae acquire functional glands, until at the seventh or eighth nomadic day almost all individuals of the three arbitrary size groups have functional

labial glands capable of a maximal secretory activity. This secretory condition persists until the time when acidophilic spinning material begins to form in the glandular portion simultaneously with the disintegration of the saccus portion of the labial gland. This is evident in the largest larvae of the tenth and eleventh nomadic days and in the smallest larvae on the twelfth nomadic day. The passage of the spinning material to the ducts of the gland occurs in the very last stages of larval development just prior to cocoon spinning and is evident in some of the largest larvae of the twelfth nomadic day. Some of these largest larvae are then already enclosed in cocoons, thus indicating their precocity in this and related aspects of development.

**E. Imaginal leg discs.**—Histological study of sectioned materials supports the conclusions from microscopic examinations and measurements of the external morphology of *burchelli* larvae as to the imaginal leg discs, concerning the time of their first appearance, relative size at different stages, pattern of development, and rate of growth. Judgments regarding development of the leg discs of the more mature larvae of the tenth, eleventh and last nomadic days were also verified by study of the internal morphology of these structures.

The leg discs first appear as paired thickenings of the hypodermis on the ventral surface of the thoracic segments (fig. 18). These structures are composed of several layers of actively dividing, basophilic-staining cells. In the course of development these discs become set off from the surrounding hypodermis by a peripodal cavity (fig. 7). As they grow, the leg discs undergo an antero-posterior extension as well as a transverse segmentation, with a corresponding enlargement of the peripodal cavity (figs. 22 and 24). The leg discs are in their most advanced state of development in the potential major worker larvae at the tenth nomadic day, in the intermediate larvae at the eleventh nomadic day, and in the smallest larvae at the last nomadic day. In this condition they are large, elongated, transversely segmented structures, generally submerged beneath the surface of the integument. Each of the three pairs of leg discs lies for the most part within one thoracic segment, but at maturity the posteriorly directed free ends of all the pairs usually extend into the next segment (fig. 24).

As the leg discs grow and become more posteriorly directed, there is a decrease in their visible surface area for they grow beneath the integument and the surface integument grows over the discs so that only a small portion of each leg disc projects above the integument. These projecting structures have been studied in detail by G. C. WHEELER (1938) who termed them 'leg vestiges'. These occurrences in leg disc development account for the fact that first in the largest and then in the upper intermediate size groups after the tenth nomadic day, no values for external leg disc areas can be recorded (table I). From this we should also expect a resulting drop in the curve representing *burchelli* leg-disc growth in terms of external measurements in the last stages of larval development (fig. 5).

**F. Dorsal vessel.**—The dorsal vessel or heart of *burchelli* larvae is a single median tube which lies just under the dorsal integument and is



surrounded by many pericardial cells, fat tissue cells and muscles. In its forward extension from its open posterior end, it first lies above the rectum in the region of the twelfth or thirteenth segment, extending to its anterior aortic region in the prothoracic segment. Here the heart bifurcates to form two anteriorly directed branches which extend ventrally into the head segment, where, after flanking the walls of the esophagus, each terminates on the side of the esophagus just dorsad to the corpora allata. These branches of the heart seem to terminate in a sinus, the fluid contents of which presumably bathe the corpora allata, the brain and other head structures.

In this species, the ostia of the dorsal vessel are found in each segment, dorsolaterally arranged, and appear to form valve-like septa. As each intersegmental region of the heart apparently is enlarged in its diameter, the heart takes on a chambered appearance.

Histologically, the heart is composed of a single layer of extremely flattened, endothelial-like cells, and its walls are surrounded by numerous minute muscles and nerves. This organ is much the same in all stages of larval development and in larvae of all the different polymorphic size groups. However, in the larvae studied, different states of contraction of the heart are evident which may be assumed to reflect its physiological condition at the time of fixation.

**G. Ovaries.**—The undeveloped ovaries of *burchelli* larvae are discernible as paired, elongated, strap-like bodies located in the middorsal region of the ninth or tenth larval segment lying between the heart and midgut. These primordia of the evidently non-functional reproductive system of the adult worker are present in larvae of all polymorphic size groups throughout development. They are extremely minute in larvae of the early developmental stages, but as development continues, mitotic divisions are evident in the ovaries and they enlarge. Two distinct regions become discernible; a central core of basophilic-staining cells, and a periphery of acidophilic-staining cells (fig. 25). The cells of both regions have distinct ovoid-shaped nuclei. The ovaries are surrounded by a fibrous network, but no oviducts or genital openings were apparent in any of the material studied.

**H. Fat tissue.**—Numerous fat cells are present in *burchelli* larvae throughout development, and a general judgment was made of the relative amount of fat present within larvae of the different polymorphic forms at different stages of development. The results of these observations indicate that the largest larvae at each successive developmental stage have relatively greater amounts of fat tissue than do either the intermediate or the smallest larvae of that same developmental stage, or the intermediate or smallest larvae of comparable body length at other developmental stages.

Apart from differences in the relative amounts of fat tissue in larvae of the different polymorphic size groups, changes were noted in the

cytology of the fat cells in larvae of all sizes throughout development. These changes include the presence, in varying amounts, of vacuoles, acidophilic-staining globules, and crystalline inclusions in the fat cells (fig. 7, 13, 15, 18, 20 and 23). These changes are believed indicative of, and related to, metabolic changes during metamorphosis of this species, but not to polymorphic differences.

## DISCUSSION

The description of the external morphology of *Eciton burchelli* herein presented conforms to and extends the general descriptions given for larvae of this species by EMERY (1899 and 1901) and G. C. WHEELER (1943). Study of the internal anatomy of the larva of this species reveals a close similarity to that of *Eciton hamatum* (TAFURI, 1951) and a general similarity to the anatomy of other ant larvae which have been described from histological studies (PÉREZ, 1902; STÆRKE, 1948; ATHIAS-HENROIT, 1947; MARCUS, 1951, and VALENTINI, 1951). The present account also confirms the brief description of the digestive tract of *Eciton burchelli* made by WHEELER and BAILEY (1925).

Adult worker populations of *Eciton burchelli* are polymorphic (W. M. WHEELER, 1910 and 1921, and EMERY, 1899). That is, all the adult individuals of a single *Eciton* colony are sterile females which between the extremes exhibit graduated differences in body size and in structural details. The adult extremes range from the largest workers, the workers major, which have huge hooked mandibles and a heavy exoskeleton, to the smallest workers, the minima, which have relatively small, feebly developed mandibles and a less heavily armored exoskeleton.

It is highly probable that the largest larvae of any stage have developed from the eggs first to be laid and first to hatch and represent the potential major workers of the mature brood. Similarly, the smallest larva presumably develop from the eggs last to be laid and last to hatch and represent the potential workers minima of the mature brood.

Study of the development of a single *hamatum* brood series (TAFURI, 1951 and 1955) revealed a distinct foreshadowing of adult polymorphism in the larval form. For example, evidence was found that during larval development the growth of the imaginal leg discs proceeds at a different rate in each of the three polymorphic size groups studied. TAFURI's results show that the growth rate of specific larval structures is describable as an allometric and not as a direct function of the overall body growth. His results showed that in *hamatum* larvae the growth rate of the leg discs was slowest in the largest larvae, intermediate in the intermediate size larvae, and fastest in the smallest larvae of the developing brood. In all three of these polymorphic types, the leg discs being the local structures best studied in this connection, the limb buds advance in a geometric

and not in a direct relationship to body length when body length is taken as the indication of overall body growth.

The evidence presented in this investigation regarding larval development of a synthetic series of all-worker brood of *Eciton burchelli* indicate that differences exist in hatching time within the distinctive brood, as well as growth differences in size and in the time at which individuals throughout the size range attain specific structural advances. From these results it is apparent that from the earliest stages of development the basis of adult polymorphic differences is established in the brood of this species.

It is significant that differences in the growth pattern of the leg discs occur in *burchelli* much as TAFURI found them to occur in *hamatum*. Also, for *E. burchelli* the ratio of quantitative changes in leg discs to body length was obtained for each of the three larval groups through the

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FIG. 1-7. — (1) Fig. 1. Representative specimens of the smallest (A), the size-graded (B), and the largest (C) polymorphic size-groups of *Eciton burchelli* larvae. 41th N. D.\* Lynch's borax-carminc whole mount. X 1.75. Fig. 2. Dorsal view of head segment showing mouth parts. L-larva\*\*, 7th N. D. Lynch's borax-carminc whole mount. X 55. Fig. 3. Side view of head and prothorax showing mouth parts and some internal structures. I-larva\*\*\*, last N. D. Lynch's borax-carminc whole mount. X 80. Fig. 4. Ventral surface of larva showing imaginal leg discs (two pairs, meso and metathoracic, in focus) and one leg vestige (mesothoracic). L-larva, 8th N. D. Bouin's preserved specimen. X 4.75. Fig. 6. Longitudinal section. S-larva\*\*\*\*, 3rd N. D. Harris' haematoxylin, eosin. X 80. Fig. 7. Longitudinal section of head and thorax. I-larva, 8th N. D. Harris' haematoxylin, eosin. X 55.

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#### LEGEND TO FIGURES

A : Anus. — AD : Antennal Disc. — B : Brain (Supraesophageal ganglion). — BC : Buccal Cavity. — Bl : Blood. — Bl' : Blood (Very granular). — CA : Corpora Allata. — CB : Cellular Breakdown products. — CD : Common Duct (Labial Gland). — Ch : Chorion. — Cu : Cuticle. — Cu' : Cuticle (Double). — DL or LD : Duct Labial Gland. — DV : Dorsal Vessel (Heart). — E : Esophagus. — EI : Esophageal Invagination (Cardiac Valve). — F : Fat. — FM : Fibrous Acidophilic Material. — FG : Frontal Ganglion. — G : Galea. — GD : Gonopodal Disc. — GL or LG : Labial Gland (Glandular Portion). — Gr : Granular Secretion (Labial). — H : Hypodermis. — Hg : Hindgut. — I : Intima. — L : Lumen filled with fine granules. — Lb : Labium. — LD : Leg Disc. — LP : Labial Palp. — Lr : Labrum. — LV : Leg Vestige (Sectional view). — LV' : Leg Vestige (Small circular structure). — M : Midgut. — M' : Midgut (Histolysis). — Md : Mandible. — MT : Malpighian Tubules. — MT' : Anlagen of Adult Malpighian Tubules. — Mu : Muscles (Surrounding Midgut). — Mu' : Muscles (Surrounding Esophageal Invagination). — Mx : Maxilla. — MxP : Maxillary Palp. — NC : Ventral Nerve Connectives. — Nu : Neurilemma. — O : Ovary. — OS : Opening of Sericteries (Labial Glands). — P : Pharynx. — PC : Peripodal Cavity. — PG : Prothoracic Ganglion. — PM : Peritrophic Membrane. — PS : Prothoracic Segment. — R : Rectum. — RN : Recurrent Nerve. — S : Saccus (Labial Gland; Sectional view of cells). — S' : Saccus (Labial Gland; Surface view of cells). — SG : Subesophageal Ganglion. — Su : Submerged Portion of Leg Disc. — VG : Ventral Ganglion. — VG' : Ventral Ganglion (Last).

\* N. D. -- "Nomadic Day".

\*\* L-larva of the largest polymorphic size group.

\*\*\* I-larva of the size-graded (Intermediate-size) polymorphic size group.

\*\*\*\* S-larva of the smallest polymorphic size group.

(1) All illustrations are photomicrographs of *E. burchelli* larvae.



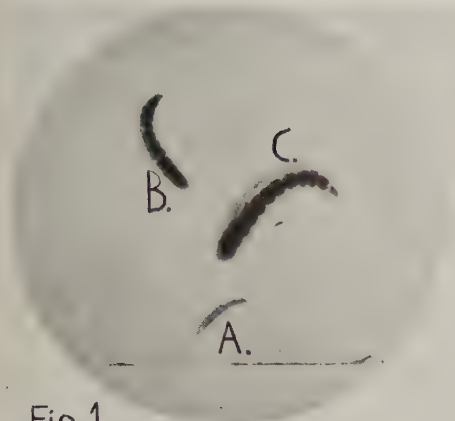


Fig. 1

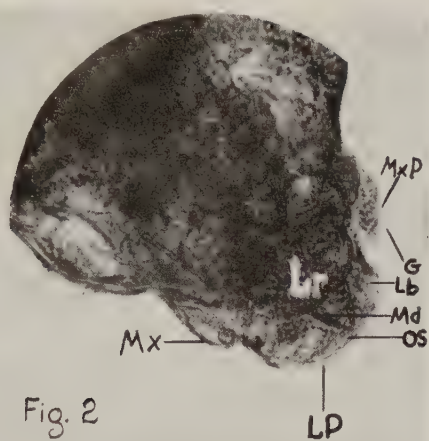


Fig. 2

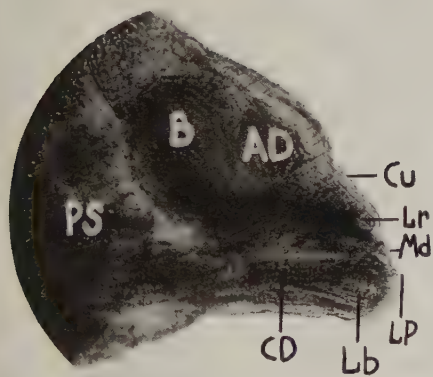


Fig. 3

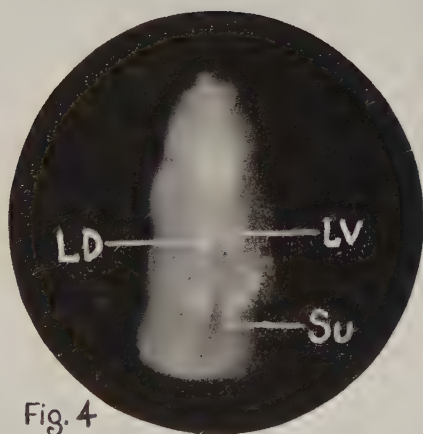


Fig. 4

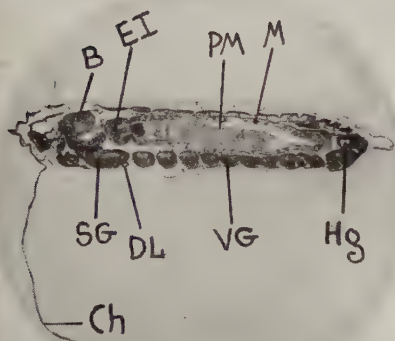


Fig. 6

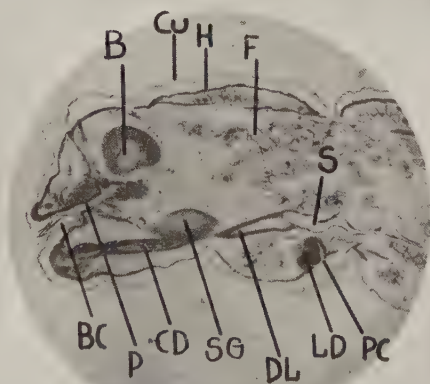


Fig. 7

polymorphic range. A graphic expression of the results indicates that the allometrically expressed growth rate is characteristically different for individuals through the polymorphic series, being slowest in the largest, somewhat greater in the intermediate and most rapid in the smallest larvae. These results might have been expected from SCHNEIRLA's (1933) confirmation and extension of MÜLLER's (1886) single observation that in *E. burchelli* the worker majors are the first individuals in each brood to eclose, the workers minima last. SCHNEIRLA (1949) has also reported that in *E. burchelli* and *E. hamatum* similar conditions prevail as to the attainment of larval maturity and enclosure in the respective polymorphic types.

The type of continuous, evenly graduated polymorphism found in the all-worker broods of these Ecitons may be understood in the light of previous studies of polymorphism of the intra- or inter-caste type which it resembles. The characteristic unique to the Ecitons, as SCHNEIRLA (1938 and 1949) has emphasized, is the occurrence of such polymorphism through very large, distinctive brood populations produced at regular and well-marked intervals throughout the year.

Differing theories have been proposed regarding the cause and time at which caste determination occurs during development of the social insects and reviews of the literature on this topic (LIGHT, 1942 *a*, 1942 *b*; W. M. WHEELER, 1908, 1910, 1933; and WILSON, 1953 *a*, 1953 *b*) draw attention to two main approaches to the solution of this problem. Caste determination may be considered to be mainly or entirely blastogenic, being established by genic factors and by the amount and quality of nutritive material in the egg and embryo (W. M. WHEELER, 1933; FLANDERS, 1946 and 1952), or it may be considered to be trophogenic and due to the quality or quantity of the diet during larval development, trophic exchanges between the adults and the developing broods being the determining factors (W. M. WHEELER, 1910 and 1933, and WILSON, 1953 *a*). A blastogenic determination, on the other hand, might be regarded as restricted to genic factors alone. More recently there has been a tendency to consider both the trophogenic and blastogenic factors as contributors to the caste determination of ants (FLANDERS, 1945). In any event, it is generally accepted that caste determination begins to be established prior to the histolytic and histogenetic processes of the pupal period of metamorphosis.

Recent experimental advances bearing upon caste determination and

FIG. 8-13. — *Fig. 8.* Longitudinal section through head and thorax of brood specimen. L-larva, 8th N. D. Harris' haemotoxylin, eosin. X 55. *Fig. 9.* Longitudinal section through posterior abdomen. I-larva, 5th N. D. Harris' haemotoxylin, eosin. X 55. *Fig. 10.* Transverse section through head. S. larva, 7th N. D. Harris' haemotoxylin, eosin. X 265. *Fig. 11.* Transverse section through abdomen. I-larva, 8th N. D. Iron alum haemotoxylin. X 55. *Fig. 12.* Longitudinal section through head. L-larva, 8th N. D. Harris' haemotoxylin, eosin. X 265. *Fig. 13.* Longitudinal section through abdomen. I-larva (Near small), 5th N. D. Harris' haemotoxylin, eosin. X 265.

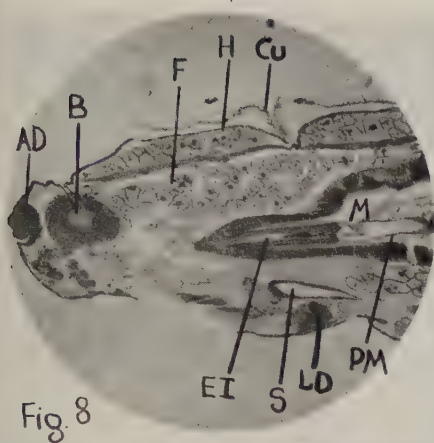


Fig. 8

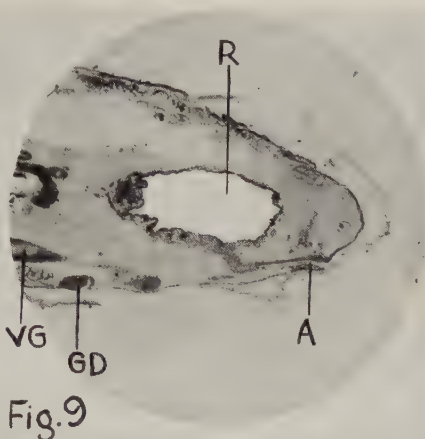


Fig. 9

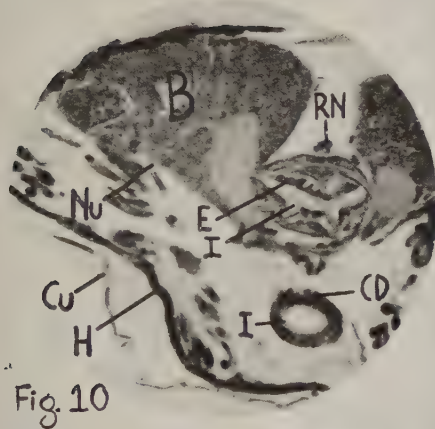


Fig. 10

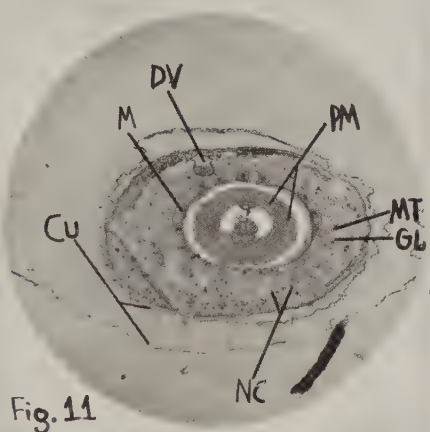


Fig. 11

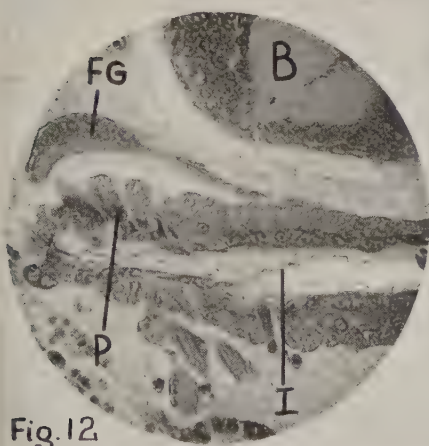


Fig. 12

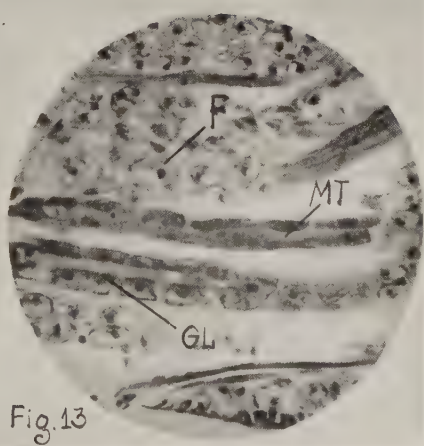


Fig. 13



polymorphism of the intercaste type in the social insects suggest that the caste of any individual is set during larval development and that nutrition and the attained size of the larvae at the time of pupation are its major determinants (WILSON, 1953 *a*, 1953 *b*). BRIAN (1951, 1952) from studies of caste determination in *Myrmica rubra*, finds results indicating that larval size at pupation, along with the size and state of development of the imaginal rudiments, particularly the leg discs, are critical to determination of queen or of worker castes.

In *E. burchelli* and *E. hamatum*, queens and workers occur in distinctively different broods as SCHNEIRLA and BROWN (1952) have reported. These investigators find indications of a differentiation established very early in development, apparently on a trophic basis. SCHNEIRLA considers it very probable that polymorphic differences in the all-worker broods may depend mainly, if not altogether, on graduated differences in trophic conditions affecting different parts of the brood series. These differences in trophic conditions could possibly depend upon differences in the order of the oöcyte maturation process, egg-laying and hatching of the eggs, and upon the time at which larval feeding begins. From field observations, he estimates that a queen of *Eciton burchelli* requires a period of about ten to twelve days to lay the more than 120,000 eggs of the distinctive all-worker broods of this species, with an intermediate peak of 3 to 4 days.

In the present studies of the larval stages of development in these all-worker broods, beyond relative differences in the overall size, size of the corresponding structures and relative differences in the time of appearance of these structures in the various members of the brood series, no evidence was found of qualitative differences in external or internal structures through the polymorphic range. However, throughout the larval series at any one time, the differences in size and volume of the larvae are consistent with what would be expected from the study of brood samples from the same brood at any earlier time. That is, in all cases, the largest larvae, presumably developed from eggs first laid and first hatched in the series, are the first to develop local structures such as the leg discs and functional organs such as the labial glands, and are the first to exhibit the respective changes of further growth in these structures. From these differences it may be concluded that the largest larvae reach each further growth stage upward to and including larval maturation, as well as

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FIG. 14-19. — Fig. 14. Longitudinal section through abdomen showing intensely basophilic-staining cells of the granular portion of the labial gland. L-larva, 10th N. D. Harris' haemotoxylin, eosin. X 265. Fig. 15. Longitudinal section through abdomen of L-larva, 10th N. D. Harris' haemotoxylin, eosin. X 55. Fig. 16. Transverse section through posterior region of head. I-larva, 3rd N. D. Iron alum haemotoxylin. X 265. Fig. 17. Longitudinal section through thorax. I-larva (near large), last Statory day. Harris' haemotoxylin, eosin. X 265. Fig. 18. Longitudinal section through prothorax. I-larva (near small), 5th N. D. Harris' haemotoxylin, eosin. X 265. Fig. 19. Longitudinal section through abdomen. I-larva (near large), last statory day. Harris' haemotoxylin, eosin. X 265.

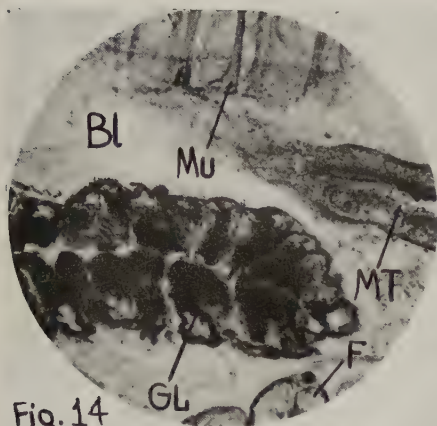


Fig. 14

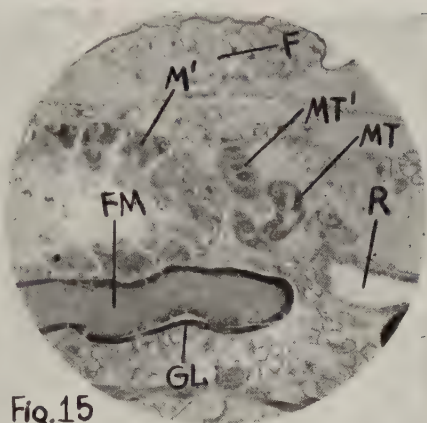


Fig. 15



Fig. 16

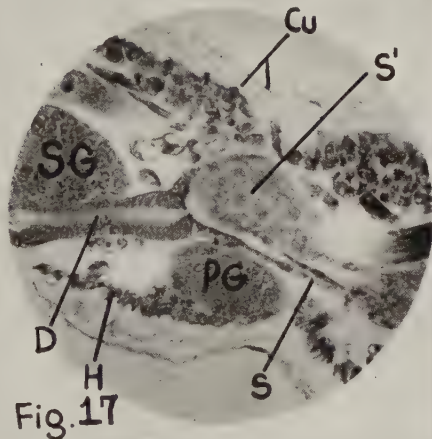


Fig. 17

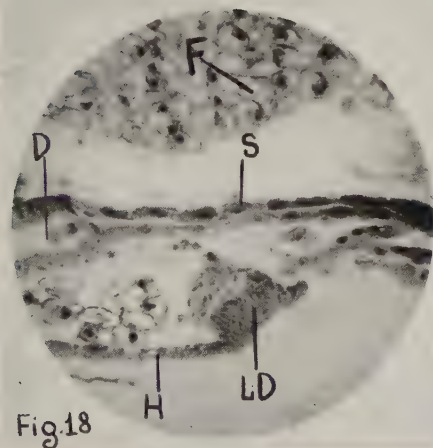


Fig. 18

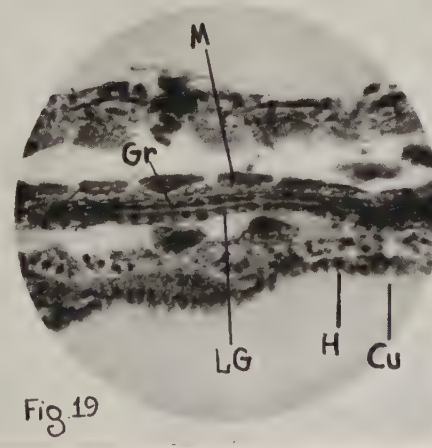


Fig. 19

spinning, in advance of the rest of the brood series. Conversely, the smallest larvae reach their fully mature state last. This statement is confirmed in some detail by evidence from the present study.

In *burchelli* the leg discs appear first in the largest larvae (last statary day), next in the intermediate larvae with roughly corresponding body size (third and seventh nomadic days), and lastly in the smallest members of the polymorphic series (eighth or tenth nomadic days). An inclusive period of about ten days is thus required for the onset of this growth change to occur in all larvae of the series. The further pattern of growth and development of *burchelli* leg discs, marked by changes such as the formation of a peripodal cavity and transverse segmentation, is similar to that previously described for other hymenoptera (PACKARD, 1897, and PRATT, 1897). Due to the fact that these structures become located beneath the surface of the integument as larval maturation approaches in *burchelli* broods, the externally visible and measurable areas of these structures then steadily diminish to a minimum.

Comparisons of larval development of *Eciton burchelli* here studied with that of *Eciton hamatum* (TAFURI, 1955) disclose only minor differences in the growth pattern of homologous structures such as the leg discs. The discs grow similarly in both species as to the increase in size, appearance of segmentation and overlapping of the posterior margins. However, one consistent difference is that in the larvae of *hamatum*, the leg discs do not grow beneath or submerge beneath the surface of the integument to any appreciable extent prior to larval maturation as they do in *burchelli*. In *hamatum* larvae increases in the size of these structures are thus externally perceptible up to the time of enclosure. The described species difference in the pattern of leg-disc growth may be related to still other differences which exist between the two species, such as variations in developmental stage among the larvae of any one cross-sectional sample. A comparative study of *E. burchelli* and *E. hamatum* in the growth rate and pattern of development of leg-disc structures will be presented in a further publication.

In the larvae of *Eciton burchelli*, the rate of growth of the leg discs is different from the overall growth rate, and is specific to this local structure. Growth of this type has been described as disharmonic or allometric growth (WIGGLESWORTH, 1950).

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FIG. 20-25. — Fig. 20. Longitudinal section through abdomen. S-larva, 10th N. D. Iron alum haemotoxylin. X 265. Fig. 21. Longitudinal section through glandular portion of labial gland in abdomen. L-larva, 8th N. D. Harris' haemotoxylin, eosin. X 265. Fig. 22. Longitudinal section through thorax showing part of submerged leg disc and disintegrating saccus portion of the labial gland. S-larva, 41th N. D. Harris' haemotoxylin, eosin. X 265. Fig. 23. Longitudinal section through thorax larval specimen showing cellular breakdown of saccus. Largest larva, 10th N. D. Harris' haemotoxylin, eosin. X 265. Fig. 24. Longitudinal section through thorax showing intact imaginal leg disc amid histolyzing tissues. L-larva, 12th N. D. Harris' haemotoxylin, eosin. X 55. Fig. 25. Longitudinal section through ovary of mature worker larva. L-larva, 10th N. D. Harris' haemotoxylin, eosin. X. 265



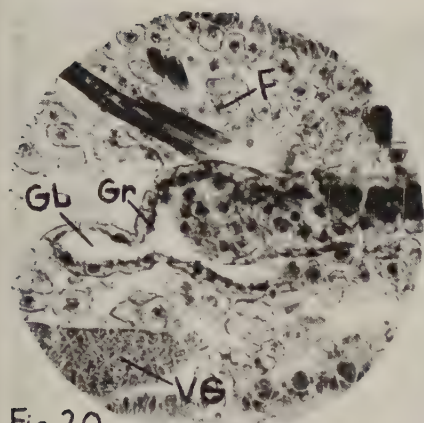


Fig. 20

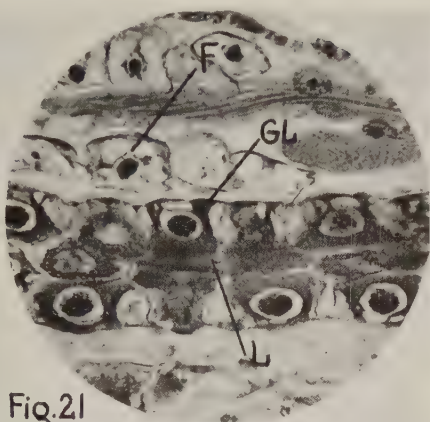


Fig. 21

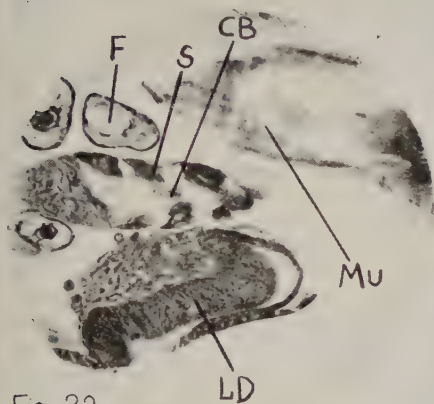


Fig. 22

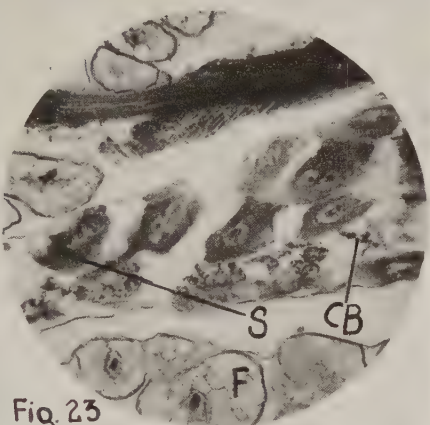


Fig. 23

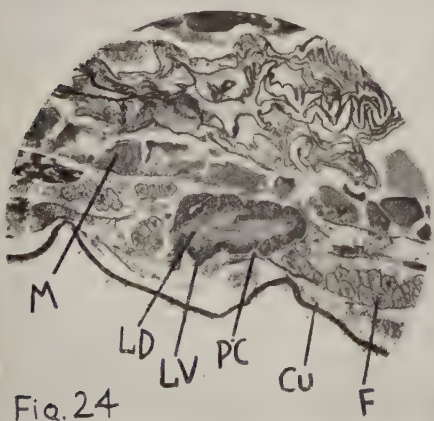


Fig. 24

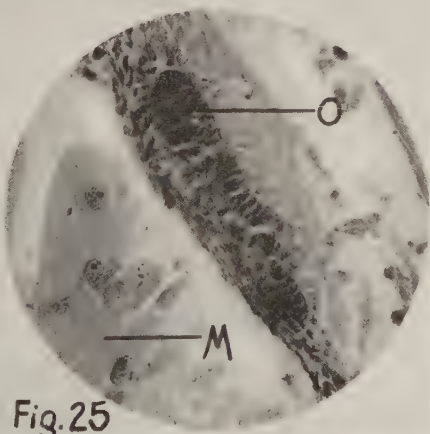


Fig. 25

Analysis of measurements of the different parts of organisms, particularly of arthropods, comparing the relative growth of these parts to the whole, have been carried out by many investigators. In 1932, HUXLEY demonstrated that a mathematical relationship exists between the growth of a part of an organism and the growth of the whole organism. He expressed this relationship in the heterogony formula,  $y = bx^k$ . Later this formula was termed the allometry formula and was revised to  $y = bx^a$  (HUXLEY, 1936) in which  $y$  equals the dimension of the part,  $x$  the dimension of the whole, and  $b$  and  $a$  are growth constants. HUXLEY showed that numerous measurements of the growth of crustacean parts, when compared to the whole, verified an allometric growth in these organisms represented by this formula. He was also able to establish the fact that polymorphism in the neuter individuals of social insects is comparable to the allometric growth of other arthropods and that his formula may be applied to both neuter social insects and arthropods in general. HUXLEY further postulated that apparent differences in structure, such as the size of the head and mandibles, among the various polymorphic forms of the social insects was a product of differential growth rate of the corresponding larval parts.

Because the present investigation utilized a synthetic population series from all-worker broods of *Eciton burchelli* in the larval period of development, the reliability of these results must be evaluated in terms of possible inter-colony differences. Possible differences effecting the growth situation, sampling techniques and relative food supplies are considered to be of major concern.

Obtaining reliable brood samples from *Eciton* colonies is difficult under the best conditions in the natural situation, in which numerous complex factors such as a gradient-wise brood distribution in the bivouac (SCHNEIRLA, BROWN and BROWN, 1954) are inevitably involved. From a general comparison of the species it seems probable that such factors impede sample reliability somewhat more extensively in the case of *E. burchelli* than in *E. hamatum*. It is therefore important to this discussion to emphasize TAFURI's (1951) findings, confirmed in this study, from studies confined to samples from a single brood series of *hamatum* which show that the relationship of overall growth to that of the local structure is expressible for that species in terms of the HUXLEY allometry formula.

By analogy, the same conditions may hold in general for *burchelli*, although with secondary differences to be expected in view of species differences such as colony and brood size, the detailed pattern of the brood microclimate in the bivouac and the like. Our present application of the allometry formula to *burchelli* may be considered too severe a test, particularly in view of the fact that the necessary use of a 'synthetic brood series', assembled from different colonies, must have magnified greatly the normal intercolony differences affecting the reliability of brood samples. For this reason it is probable that the quantitative results concerning the relationship between body length and leg-disc size were somewhat too

widely spread for a convenient statistical treatment. When an analysis of a single brood series can be made for *burchelli*, it is to be expected that much the same condition will be found for that species as for *hamatum*.

The developmental changes in the labial glands of *Eciton burchelli* larvae herein described are not unique to this species and closely parallel those described by VALENTINI (1951) for *Componotus silvaticus*, also a cocoon-spinning form. VALENTINI investigated the morphological variations of different species of ant larvae in collection with species adaptations to arid, normal or humid environments. According to him, the various morphological modifications and functional properties of the labial glands during larval development are related to the type of life situation characteristic of the species, whether the pupa is open or closed, or more specifically, whether the species is a cocoon-spinning form or not. VALENTINI concluded that apparent changes in activity of the labial glands were not directly related to the environmental conditions, but rather to the phylogenetic position of the particular species being studied. However, these may not prove to be real alternatives.

The importance of the labial glands in the social insects has long been recognized. To then W. M. WHEELER (1910) and others have attributed an important role in the trophic processes of the social insects. The times at which these glands first become functional in *burchelli* larvae, and their two-fold production of first a fine, basophilic-staining secretion and secondly, the precursor of the spinning material, suggest that the function of these glands is involved to an important extent in the brood-stimulative effects found by SCHNEIRLA (1938, 1952) to be critical for major changes in the colony behavior cycle.

Behavioral studies of *Eciton hamatum* and *Eciton burchelli* by SCHNEIRLA (1938, 1957) revealed that a distinctly increased level of colony excitation, manifested by the onset of adult predatory raids and greatly augmented 'trophallactic' relations between brood and adults, begins at the end of the statary phase, continues into the nomadic phase, and reaches its peak at larval maturity, a day or so before cocoon spinning occurs. The stimulative effect of the brood on the colony then drops away very sharply, and after the first few days of the next statary phase reaches a minimum with a limited rise near the end of the statary phase (SCHNEIRLA, 1952). At the end of this phase, emergence of the callows occurs, and once again a sharp increase in colony stimulation occurs, with colony nomadism as its main effect.

The nomadic phase in *E. hamatum* has a mode of 16 days while that of *E. burchelli* is three to four days shorter and more variable. It has also been established that the peak of raiding activity resulting in an over-abundant food supply begins at an earlier 'phase-day' age in *burchelli* colonies, that is, at approximately the eighth or ninth nomadic day. In *hamatum* this peak in raiding activity begins at approximately the twelfth or thirteenth nomadic day.

In *E. burchelli* the labial glands first become functional in the largest



larvae of the last statary and early nomadic days. Soon afterward, the intermediate and smallest larvae of successive nomadic days have functional labial glands, and by the seventh or eighth nomadic day all larvae of the different polymorphic size groups have functioning labial glands producing salivary secretion. Although the significance of this labial (or salivary) secretion for trophic and stimulative relations between brood and colony remains to be worked out, it is of interest to note that the time at which labial gland function rises to a high level coincides with the beginning of a peak of raiding activity indicated for this species at the eighth or ninth nomadic day. Furthermore, it is significant that the change in function of this gland from its primary secretory function to the production and accumulation of the precursor of the spinning material begins in the largest larvae on the tenth nomadic day, and in the intermediate and smallest larvae on subsequent nomadic days. This coincides with the time at which these respective polymorphic forms are observed to drop off in their feeding activities, although the stimulative effect of the larval brood on the adult population remains at a high point until the major part of the brood is enclosed. These results regarding larval feeding activities were obtained from field observations and laboratory studies of *E. burchelli* by SCHNEIRLA (1949).

The significance of these developmental changes in the functional activity of the labial glands of *E. burchelli* therefore cannot be overlooked as a probable major factor underlying changes in the level of colony excitation and raiding activity during the late statary and entire nomadic phases. Depending upon the extent of raiding activity of the adult workers in *E. burchelli* colonies, there is a decided variance in the amount of food available at the onset and during the development of an all-worker brood. On the basis of SCHNEIRLA's (1938, 1957) theoretical conclusions that the stimulative effect of the larval brood plays a major part in the continuation of the nomadic phase (once this phase is initiated through callow-brood stimulative effect) to its completion, these glands play an important part in the process. It is probable that the time at which they begin to secrete in the larvae has much to do with the onset and increase of feeding (brought about by an increased amount of raiding activity and an abundance of food) admitting an acceleration in growth which further increases the brood stimulative effect. Relative differences in their function may be considered a factor in the differential growth rate of the larvae and more specifically of larval structures such as the leg discs, as influenced by characteristic differences in the capacity of the larvae for feeding.

The first appearance of the imaginal leg discs corresponds significantly with the time at which the labial glands evidently become functional in larvae of the respective different size groups, as reported in terms of the 'phase-day' age. This is evidently a relatively strict correspondence, beginning with the first appearance of leg-disc development in the largest larvae of the series on the last statary day, when only these larvae have

functional labial glands. SCHNEIRLA's (1949, 1952) field investigations show that at this time the general level of raiding activity of the colony is still low although somewhat increased over preceeding days, and consequently the amount of food available in the bivouac is considerably less than in the nomadic phase. But when the smallest larvae begin to develop leg discs about the eighth nomadic day, all larvae of the developing *burchelli* brood have functional labial glands, raiding activity is high and the amount of food being brought into the colony is greater now than at any other time in the nomadic phase of activity.

It has been ascertained that during larval development in holometabolous insects, the growth rate and extent of development of the imaginal leg discs is dependent in part upon certain external factors (BODENSTEIN, 1939, 1941 and 1953). Among the most important of these factors are the relative amounts of available food, oxygen supply and the temperature of the environment. It therefore may be of some importance in considering the results of the present investigation, to review the afore-mentioned experimental evidence. It is apparent from experimental studies, that unless certain external requirements are present at a critical time (which is probably specific for each species, and perhaps for each structure), the expression of the potencies of these imaginal structures will be altered in some way (BODENSTEIN, 1939 and 1953, JU-CHI and YU-LIN, 1936; KAJI and OGAKI, 1953, and SHULL, 1937).

In view of these considerations, it is important to note that SCHNEIRLA *et al.* (1954) have found the army ant bivouac, or temporary nest of the nomadic phase, a relatively stable environment for the larval brood, leveling off environmental extremes such as lower nocturnal temperatures which might retard brood development. It also appears significant that, as these investigators report, the highest temperatures of the bivouac (ca. 29-30° C.) are maintained near its center, and more specifically, as JACKSON (1957) has subsequently found, a temperature gradient typically exists in the bivouac with its peak in the central area. Furthermore, a gradient normally exists in the distribution of larvae in the bivouac (SCHNEIRLA, 1938; SCHNEIRLA and BROWN, 1950) with the smallest larvae held centrally and the largest peripherally. In view of these facts, it is apparent that the differential microclimate typically operating for the different size-groups of the brood population is adequate to support the respectively different rates of development it was found characteristic of them. In other words, the smallest larvae, which evidently have the fastest rate of larval development, are usually located near the center of the bivouac where the highest temperatures prevail; the largest larvae, evidently with the slowest growth rate, are located marginally where the lowest bivouac temperatures prevail during the nomadic phase.

It is probable that differences in function of the labial glands depend upon their histologically different conditions in the brood population though larval development, as indicated in this study. Also, at different developmental stages other conditions governing food-intake may

account to an important extent for the fact that a differential growth rate seems to prevail among the larvae. The above ecological considerations suggest that once the smallest *Eciton burchelli* larvae are capable of feeding, situated in a higher temperature, they are relatively more active and consume more food in relation to their body size than do larger larvae. The existence of a differential growth rate of structure such as the leg discs in the polymorphic size-groups of *burchelli* larvae is consistent with the results of experimental studies of caste determination in the social insects. Such studies reveal that clues to the underlying mechanism of polymorphism point to the critical role of size and volume of larvae and the relative size and degree of development of structures such as the imaginal leg discs and wing buds at the time of pupation (BRIAN, 1951, 1952).

### SUMMARY AND CONCLUSIONS

1. The study of external and internal anatomy among larvae in the large polymorphic all-worker broods of *Eciton burchelli* indicates that although there are no identifiable qualitative differences among the larvae of any one brood sample in their general or detailed structure, there are consistent differences within any brood series as to the time of appearance of both general and detailed structural changes, as well as differences in relative growth rate through the polymorphic brood populations.

2. Caste differences are found for the time of appearance of both external structures such as mouth parts, antennal discs, imaginal leg discs and gonopodal discs and internal structures such as the alimentary canal the Malpighian tubules, the central and stomatogastric nervous systems, the corpora allata, the labial glands, dorsal vessel, ovaries and fat tissue. These studies were carried out analytically in some detail for the leg discs among external structures and for the labial glands among internal structures.

3. Detailed anatomical and histological studies of the 'synthetic-series' of specimens representing brood samples of different colonies at intervals through the nomadic phase indicate that no one characteristic of external or internal structure can be used to distinguish larvae occupying different positions in the polymorphic series. Rather, in a brood sample taken at any one time in the nomadic phase, a graduated series of measurements is obtained with respect to size and degree of development of any external or internal structure. Furthermore, in samples taken at successively different times, an overlapping of the respective graduated series of measurements is obtained.

4. From these findings it is concluded that the chief differences to be found in a brood cross-section taken at any one time lie in the relative development of individuals through the series, with individuals of the largest overall size most advanced, those of the smallest overall size least advanced, and individuals of intermediate size correspondingly advanced.



Accordingly, external structural changes in certain cuticular modifications in mouth parts, and in the leg discs, and internal changes as in the labial, glands, appear first (*i.e.*, at an earlier 'phase-day') in the larvae of greatest overall size, next in larvae of intermediate size, and last in larvae of the smallest size.

5. The significance of the developmental status of labial-gland structures among of the polymorphic series, in relation to the differential growth rate of structures such as the imaginal discs, is considered in view of inferences as to functional changes in the light of previous studies of insect polymorphism.

Evidence from a detailed study of the development of the leg discs and of the labial glands indicates that these structures develop at the slowest rate in the largest larvae, at a somewhat faster rate in the intermediate larvae, and at the fastest rate in the smallest larvae. Present evidence indicates that, as TAFURI found in the larval brood of *Eciton hamatum*, the HUXLEY allometry formula may also apply to the larval brood of *Eciton burchelli*.

6. This evidence is interpreted as supporting the hypothesis that the first-laid eggs in any one normal (*i.e.*, all-worker) brood of *Eciton burchelli* are first to hatch and at any one time thereafter are most advanced in their development, the last-laid eggs are last to hatch and at any one time thereafter are least advanced in their development, with eggs laid at intermediate times correspondingly differentiated according to their respective times of appearance in the colony. It is also concluded that, by virtue of differential growth rates in the brood, the time differential at egg-laying is considerably reduced at larval maturity, in the attainment of this stage by the largest and by the respectively smaller members of the polymorphic brood series of *Eciton burchelli*.

7. Evidence from a detailed study of the developmental history of the labial glands in this investigation, considered in its relevance for salivary-gland and spin-gland functions, is found to support conclusions made by SCHNEIRLA from his investigations with respect to the significant role of stimulative and trophic properties of the larval brood for colony behavior.

### Résumé.

L'étude de l'anatomie, interne et externe, des larves d'un couvain polymorphe "all-worker" d'*Eciton burchelli* indique que, malgré le manque de différences significatives entre les structures globales ou partielles des individus appartenant aux divers groupes polymorphes, il existe des différences importantes dans la courbe de croissance parmi les individus des populations polymorphes. Des différences dues à la caste se manifestent lors de l'apparition des structures externes telles que les pièces buccales et les disques imaginaux des antennes, des pattes et des gonopodes. Des différences se manifestent également par des structures internes telles

que le tube digestif, les tubes de Malpighi, le système nerveux, les glandes labiales par exemple. En considérant une série complète du couvain entier prise à n'importe quel moment de la phase de développement, on a trouvé que les individus les plus gros étaient les plus avancés, ceux de volume moyen étaient moins avancés, et ceux de petit volume étaient les moins avancés.

Les résultats d'une étude détaillée du développement des disques imaginaires des pattes et des changements cytologiques se produisant dans les glandes labiales indiquent que les structures se développent le plus lentement dans les larves les plus grosses, un peu plus rapidement dans les larves de volume intermédiaire et le plus rapidement dans les larves les plus petites.

Les résultats d'une étude détaillée de l'ontogenèse des glandes labiales, considérées en rapport avec leurs fonctions de glandes salivaires et de glandes séricigènes, confirment les conclusions de SCHNEIRLA acquises au cours d'enquêtes antérieures au sujet du rôle important des propriétés stimulantes et trophiques du couvain larvaire dans le comportement global de la colonie.

### **Zusammenfassung.**

Untersuchungen der inneren und äusseren Anatomie von polymorphen "All-worker" Larven des *Eciton burchelli* Stammes zeigen keine erkennbaren Unterschiede qualitativer Art in der allgemeinen oder Einzelstruktur zwischen den verschiedenen Grössenklassen, hingegen konstante Unterschiede in der relative Wachstumsgeschwindigkeit.

Zur Zeit des Auftretens äusserer Strukturen wie Mundteile, Antennensprossen (scheiben) und imaginärer Beinsprossen (scheiben), ebenso innerer Strukturen wie Labialdrüsen weisen die Gruppen Unterschiede auf.

Betrachtung einer gesamten Zucht zu einem beliebigen Zeitpunkt innerhalb der Entwicklungsphase zeigte, dass Individuen der höchsten Grössenklasse am weitesten fortgeschritten waren, Individuen von mittlerer Grösse etwas weniger entwickelt und solche von der geringsten Gesamtgrösse den geringsten Fortschritt aufwiesen.

Einzeluntersuchungen über die Entwicklung imaginärer Beinknospen und über die cytologischen Veränderungen in den Labialdrüsen zeigen, dass diese Strukturen sich am langsamsten in den grössten Larven entwickeln, etwas schneller in der mittleren Grössenklasse und am raschesten in den kleinsten Larven.

Im Rahmen dieser Arbeit wurde eine Untersuchung der Entwicklungsgeschichte der Labialdrüsen in Bezug auf ihre Bedeutung für Speicheldrüsen und Spinndrüsenfunktionen durchgeführt, es zeigte sich, dass von SCHNEIRLA auf Grund früherer Untersuchungen gezogene Schlüsse, die bedeutsame Rolle der stimulierenden und trophischen Fähigkeiten der Larvenzucht für das Kolonieverhalten betreffen, bestätigt werden können.

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VERGLEICHENDE ANATOMISCH - HISTOLOGISCHE  
UNTERSUCHUNGEN AN *LEPISMA SACCHARINA*  
LINNÉ UND DER MYRMECOPHILEN *ATELURA*  
*FORMICARIA* HEYDEN  
(BEITRAG ZUR MYRMECOPHILIE — ZWEITER  
ABSCHNITT)

VON

LOTHAR POHL

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4. — *Das Integument.*

Die körperbedeckende Schicht von *Lepisma saccharina* und *Atelura formicaria* ist einfach gebaut. Nur bei *L. s.* finden sich in den Schuppen fein verteilt granulierte Pigmente, welche die Dunkelfärbung bzw. den Silberglanz des Tieres verursachen. Die gelblich weiße Farbe von *A. f.* dürfte auf die verschiedene Stärke und auf die wahrscheinlich durch das Alter bedingten konsistenzuellen Veränderungen der Cuticula zurückzuführen sein, da frischgehäutete Tiere reinweiß erscheinen. Gekörnte Pigmente sind nicht festzustellen. Es handelt sich hier um eines der zahlreichen Beispiele für Pigmentlosigkeit bei subterrestrisch lebenden Tieren und Höhlenbewohnern, die als regressive Veränderung mit der Lebensweise in Zusammenhang gebracht werden kann.

Der Wasserhaushalt freilebender *L. s.* wird gemäß dem Aufenthaltsort dieser Tiere mehr gefährdet sein, als der der myrmecophilen *A. f.* mit einem nahezu konstant gehaltenen Luftfeuchtigkeitsgrad in den Ameisennestern. Es überrascht deshalb nicht, daß die Cuticulaschichten

von *L.s.* mächtiger entwickelt und härter sind als die von *A. f.*, die eines derartigen Transpirationsschutzes weit weniger bedarf.

Eine quer zur Körperlängsachse verlaufende Fältelung der Intersegmentalhäute scheint mir entgegen der von KÜHNELT (1928) bei Coleopteren und Lepidopteren vertretenen Ansicht, wonach sie ein Verkleben der Intersegmentalhäute verhindern soll, hier eher eine Einrichtung zur Vermeidung von Spannungszuständen zu sein, wie sie beim Abbiegen des Körpers oder beim Aufrichten der Schilder auftreten.

Hypodermale Häutungsdrüsen fehlen beiden Tieren. Alle Zellen der Hypodermis können ins Häutungs geschehen eingreifen. Da sich zwischen den rhythmisch abscheidenden Lamellen der neuen Cuticula Exuvialflüssigkeit vorfindet, darf mit Sicherheit angenommen werden, daß sie hier nicht nur vor der Bildung der neuen Cuticula, sondern auch in den Abscheidungsintervallen der einzelnen Lamellen erzeugt wird. Das Gefüge der neuen Cuticula ermöglicht den Durchtritt der Exuvialflüssigkeit, während die impermeable Exuvie von ihr angedaut und abgehoben wird.

### 5. — Die Muskulatur.

Körper- und Extremitätenmuskulatur stimmen bei beiden Objekten im wesentlichen überein. Starke Beinmuskeln ermöglichen beiden Tieren, sich gewandt und schnell ihren Verfolgern zu entziehen. Für *A. f.* erweist sich der gedrungene kurze Körper, der einem Zugriff leicht entgleiten kann, beim myrmecokleptischen Nahrungserwerb als besonders vorteilhaft. *A. f.* kann zum Unterschied von *L. s.* dank der günstigen Schwerpunktslage seines Körpers Kurven und Kreise auf engstem Raum beschreiben. Oft, so z.B. beim Putzakt, lassen sich bei beiden Objekten ruckartige seitliche Krümmungsbewegungen beobachten. Sie werden durch das Vorhandensein sekundärer lateraler Sklerite und der damit verbundenen höheren Zahl an streckbaren Intersegmentalhäuten möglich gemacht. Kräftige, von der Stirnseite der vorangehenden Segmente ausgehende Muskelstrahlenbündel inserieren an ihnen.

Eine rasche Beweglichkeit ist allen Lepismatiden eigen. Sie wird deshalb für *A. f.* keine zusätzlich erworbene Fähigkeit im Sinne einer Anpassung an die Myrmecophilie sein. Sicher aber ist sie begünstigende, ja mit entscheidende Voraussetzung für das Zustandekommen eines derartigen Synoekieverhältnisses mit Ameisen.

### 6. — Drüsen des Kopfes.

Kopfnephridien sind bei beiden Objekten vorhanden. Sie bestehen aus sezernierenden Blasen und paarigen ektodermalen Ausführgängen, deren Epithel auch Sekret produzieren kann. Ihre gemeinsame Mündung liegt zwischen Hypopharynx und Unterlippe. Nur bei *A. f.* dagegen ließ sich



ein medianes Kugeldrüsenpaar mit getrennten Ausführungsgängen im Maxillarbereich feststellen. Eine Verbindung der Lumina beider Kugeln besteht

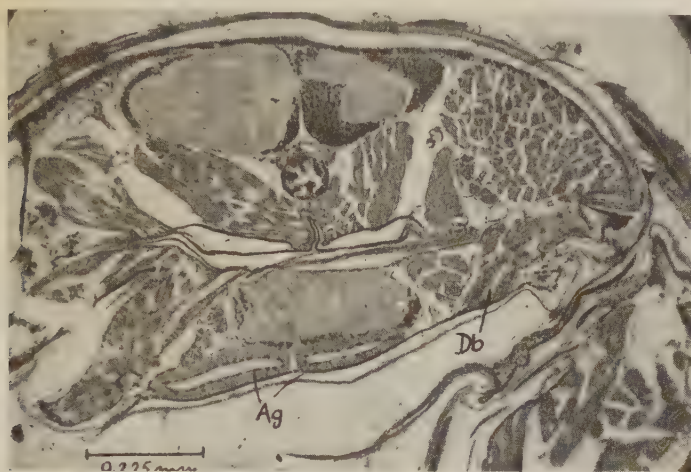


ABB. 11. — *Lepisma saccharina*.

Querschnitt durch die hintere Kopfregion mit Pharynx, Ausführungsgängen (Ag) und Drüsenblasen (Db) des Kopfnephridiums.

nicht. Ebenso fehlt ein Zugang zu den Ableitungsrohren der Kopfnephridien. Nach den biologischen Beobachtungen scheint es eher möglich, daß diese Drüsen bei *A. f.*, die zum Unterschied von *L. s.* ein geradezu übersteigertes Reinlichkeitsbedürfnis hat und alle paar Minuten Antennen, Beine und Schwanzanhänge mit den Mundgliedmaßen putzt (WYGODZINSKY, 1941), im Dienste des Reinigungsinstinktes stehen, als daß sie für die Verdauung notwendig wären.

Während *L. s.* Corpora cardiaca in der paarigen Anordnung an der Aortenwand besitzt, fehlen sie bei *A. f.* Solange über die Funktion dieser Organe keine völlige Klarheit herrscht, fehlt neben der Berechtigung zur Annahme analoger Bildungen bei *A. f.* die Grundvoraussetzung für eine vergleichende Betrachtung im Hinblick auf die Lebensweise der Tiere.

Das gleiche mag für die bei beiden Tieren fehlenden Corpora allata gelten. Es wäre denkbar, daß sie in die Cerebralsubstanz verlagert worden

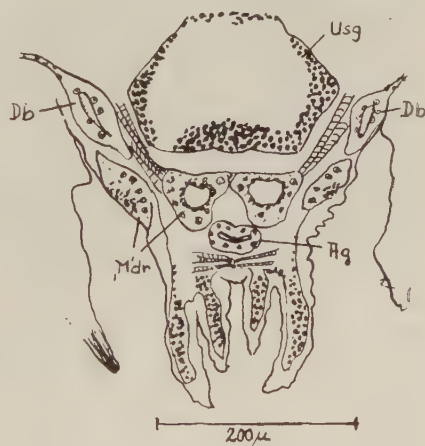


ABB. 12. — *Atelura formicaria*.

Ausführungsgang (Ag) und Drüsenblasen (Db) des Kopfnephridiums und maxillare Drüsenblasen (Mdr) querschnitt. Usg-Unterschlundganglion.

sind und als eigenkörperliche Organe nicht faßbar wären, bzw. daß bestimmte Gehirnpartien ihre vielseitigen, noch nicht restlos geklärten Funktionen übernehmen könnten. Andererseits könnte die Ursache ihres "Fehlens" im Zusammenhang mit einer ihrer Funktionen, der bei Epimetabolen primitiven, auf einfache "imaginipetale Merkmale beschränkten Metamorphose" (WEBER, 1948) stehen.

Speicheldrüsen sind bei *L. s.* und *A. f.* in gleicher Gestaltung vorhanden. Sie erstrecken sich vom Kopf bis zum Beginn des Mesothorax nach hinten. Es sind paarige, acinöse Drüsen, die in den Ausgang der medianen Tube des Kopfnephridiums getrennt münden. Im Prothorax haben sie ihre größte Ausdehnung.

## 7. — Das Nervensystem.

Die zufolge unterschiedlicher psychischer Beanspruchung erwarteten Abweichungen im Gehirn beider Tiere werden durch die anatomischen Befunde bestätigt. Eine mächtige Ausbildung der protocerebralen Gehirn-

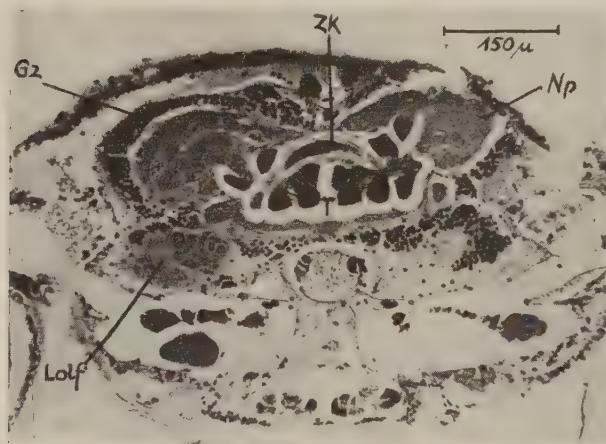


ABB. 13. — *Lepisma saccharina*.

Querschnitt durch den protocerebralen Abschnitt des Gehirns mit Trauben (T), Zentralkörper (Zk) und angeschnittenem Lobus olfactorius (Lolf). Np-Neuropilem, Gz-Globulizellen.

partie ist beiden Tieren gemeinsam. Allein ein großzügiger Vergleich, soweit er unter Berücksichtigung der relativen Gehirngröße bei beiden Objekten und unter Abzug der Lobi optici bei *L. s.* möglich ist, zeigt, daß die protocerebrale Neuropilem-substanz von *L. s.* volummäßig nicht an die von *A. f.* heranreicht. Dieser Feststellung entspricht als sichtbarer Maßstab für die Menge der Neurone die Anzahl der Globulizellkerne, die bei *L. s.* auf

bestimmte Stellen der Gehirnoberfläche beschränkt, erkennbar hinter der von *A. f.* zurückbleibt.

Wenn der bereits weitgehend erwiesene Zusammenhang zwischen Corpora pedunculata und psychisch assoziativen Fähigkeiten bei Insekten rechtmäßig besteht, so darf er mit gleicher Berechtigung auf die von BÖTTGER (1910) den Corpora pedunculata als analog erkannten "Trauben" bei Lepismatiden erweitert werden. Unter dieser Voraussetzung und der weiteren, daß die relative Größe als Kriterium für psychische Leistungen

gelten darf, können auf Grund einer mächtigeren Ausbildung der protocerebralen Trauben bei *A. f.* höhere Fähigkeiten angenommen werden. Diese Befunde stehen im Einklang mit der Erwartung seitens der Lebensweise der Tiere.

*A. f.*, die mit dermaßen hochstehenden Insekten wie es Ameisen sind in einer Synoekie lebt, werden zwangsläufig höhere psychische Leistungen abgefordert als *L. s.* unter ihresgleichen. Sie bestehen in komplizierten Orientierungsvorgängen und raschem Reaktionsvermögen bei der spezialisierten Form des Nahrungserwerbs und der Begegnung mit Ameisen.

Der Verlust des Sehvermögens bei *A. f.*, der in der Dunkelheit der Ameisennester keinen Nachteil darstellt, wird nach dem Grundsatz biologischer Notwendigkeit zumindest teilweise durch eine erhöhte Leistungsfähigkeit anderer Sinne ausgeglichen sein. Diese Vermutung wird durch den anatomischen Befund gestützt. Die deutocerebralen Lobi olfactorii der blinden *A. f.* sind mässiger als die von *L. s.* Erwähnung verdienen bei jenem Objekt die dicken Glomeruliballen im Antennalmark und die starken Nervi antennales. Ein kräftiger Tractus olfactorioglobularis von den Antennalgglomeruli zu den Stielen und damit zu den protocerebralen Trauben ist ein Hinweis dafür, daß dem Protocerebrum neben assoziativen auch receptive Fähigkeiten innewohnen.

Die Untersuchungsergebnisse an *A. f.* deuten gemäß den Erwartungen auf spezialisierte Antennalfunktionen hin.

*A. f.* ist dem Fluchttypus der Myrmecophilen zuzuordnen. Mimetische Einrichtungen zur Täuschung der Ameisen sind nicht vorhanden, wohl aber Anpassungen an die Myrmecokleptie und die Umgebung. Die Tiere halten sich verborgen und vermeiden jede Berührung mit Ameisen außer zum Erwerb von Nahrung. Auf Grund ihrer Beweglichkeit und Wendigkeit sind sie von Ameisen schwer zu erreichen. Beim Zusammentreffen einer Ameise mit *A. f.* versuchen die Tiere durch gegenseitiges Abtasten mit den Antennen ein körperhaftes Tastbild voneinander zu erhalten. Das stellte WYGODZINSKY (1941) auch wiederholt zwischen zwei *A. f.* fest, während *L. s.* aneinander vorbeihuschen, ohne sich Beachtung zu schenken.

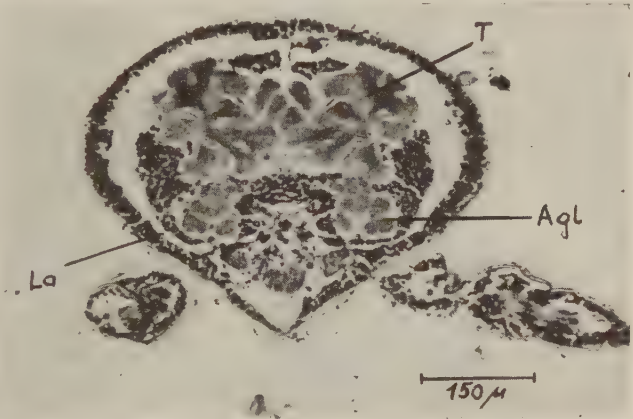


Abb. 14. — *Atelura formicaria*.

Querschnitt durch das vordere Protocerebrum mit Trauben (T).  
Ventral die Lobi antennales (La) mit Antennalgglomeruli (Agl).



Ich bin der Ansicht, daß ein Tasteindruck von einer einzelnen Ameise bei *A. f.* schneller entsteht als ein sicheres Tastbild von *A. f.* bei der Ameise, und daß dieses bei *A. f.* eine sofortige Fluchtreaktion bzw. eine Fluchtbereitschaft zur Folge hat. Bei sich fütternden Ameisen entsteht für *A. f.* ein ganz anderes, sicher als Engramm eingprägtes Tastbild. Ein Abtasten von Seiten der Ameisen unterbleibt. Sie sind mit ihrem Fütterungsakt so beschäftigt, daß sie selbst dann nicht reagieren, wenn sich *A. f.* zwischen sie drängt und ihnen den Futtertropfen wegsaugt (JANET, 1898). Eine Verfolgung der *A. f.* wird nicht aufgenommen.

Zusammenfassend läßt sich sagen, daß sich *A. f.* in Anpassung an die

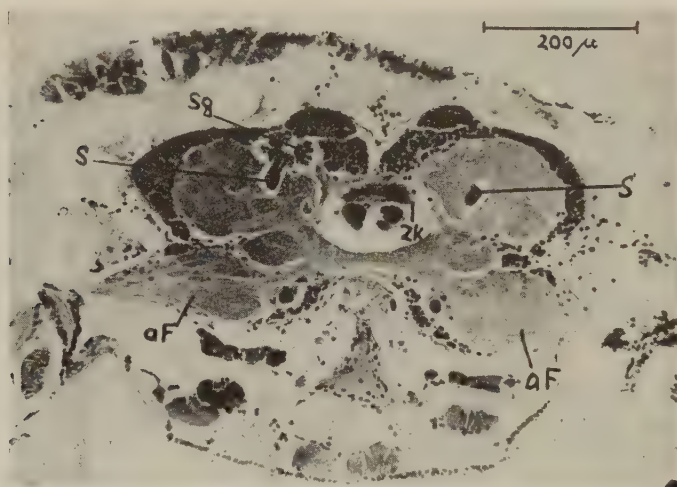


Abb. 15. — *Lepisma saccharina*.

Querschnitt durch das rückwärtige Protocerebrum mit Stielglomeruli (Sg), Stielen (S), Zentralkörper (Zk) und anten-nalen Fasermassen (aF).

Synoekie mit Ameisen ganz zu einem Tasttier spezialisiert hat, was auch die anatomischen und histologischen Befunde in der Differenzierung der deutocerebralen Antennalzentren bestätigen.

*A. f.* ist der einzige blinde Vertreter der Lepismatiden. Da kein Rudiment der Augen festzustellen ist, gelingt es nicht, den Weg der Reduktion, falls überhaupt eine erfolgt ist, aufzuzeigen. Man wird aber, wenn man die für zahlreiche andere Cavernicolen als erwiesen geltende Tatsache der Rückbildung des Gesichtssinnes für dieses Objekt teilt, einer dermaßen abgeschlossenen Regression, wie sie aus dem negativen Befund hervorgeht, in der phylogenetischen Entwicklung von *A. f.* die Stellung einer primären Veränderung einräumen müssen.

Das Zusammenrücken des letzten Thorakal- und ersten Abdominalganglions des Bauchmarks ist wahrscheinlich im Sinne einer höheren Spezialisierung zu deuten (vergl. GÖSSWALD, 1953; KRUG, 1954 b. Hymenopteren).

UEBERSICHT UEBER ANATOMISCHE UND HISTOLOGISCHE BEFUNDE.

LEPISMA SACCH.

ATELURA FORM.

Cuticula hart und dick.  
 silberglänzende Schuppen.  
 Oenocyten fehlen.  
 sekundäre Sklerite vorh.  
 Kopfnephridien vorhanden.  
 fehlt.  
 Corpora cardiaca.  
 C. allata nicht feststellb.  
 Lobi optici.  
 z. T. freie Neuropilemfelder an Oberfläche.  
 „Trauben“  
 unpaares Frontalorgan.  
 paarige Frontalorgane.  
 Antennallobi relativ gering entwickelt.  
 zweiteiliges Antennalzentrum.

C. weich und dünner.  
 pigmentlose Schuppen.  
 fehlen.  
 vorhanden.  
 vorhanden.  
 medianes Kugeldrüsenpaar  
 (Mündg. an Maxillen).  
 fehlen.  
 nicht feststellbar.  
 fehlen.  
 Ganglienzellrinde breit  
 ohne freie Felder.  
 vorhanden.  
 fehlt.  
 vorhanden.  
 mächtig entwickelt.  
 einheitliches Antennalzentrum.

**Zusammenfassung.**

*Atelura formicaria* zählt zum Fluchttypus der Myrmecophilen. Eine strenge Bindung an Ameisen besteht nicht. Es handelt sich um einen Fall von Synoekie, bei dem *A. f.* Nutznießer der sozialen Fütterungsinstitute der Ameisen ist und der seinen Grund im Anpassungskomplex von *A. f.* allein hat. Duldungsinstitute von Seiten der Ameisen wie bei echten Symphilen scheiden hier mit der gleichen Sicherheit aus, wie man phylogenetisch in langer Vererbung entstandene Instinktmechanismen für die Synoekie mit Ameisen bei *A. f.* annehmen darf. Es überrascht nicht, daß bei *A. f.* morphologische Abweichungen vom Bau freilebender Lepismatiden in der Bedeutung mimetischer oder wehrhafter Merkmale fehlen. Dafür haben die vorliegenden Untersuchungen anatomische und histologische Besonderheiten erbracht, die mit der Lebensweise in kausalem Zusammenhang stehen und als Umgestaltungen bzw. Anpassungen nach zwei Richtungen hin gewertet werden müssen.

Pigmentlosigkeit der Körperbedeckung und Blindheit bei *A. f.* werden Verlustkonvergenzen zu Cavernicolen sein und als Folge der hypogäen Lebensweise unabhängig von Myrmecophilie entstanden sein.

Als Anpassungen an die Ameisen selbst oder an die durch sie verursachten ökologischen Gegebenheiten im Nest bestehen anatomische Abweichungen von frei— bzw. untereinanderlebenden Lepismatiden.

Dazu zählen Anpassungen des Verdauungsapparates an die spezielle Technik des Nahrungserwerbs und die stoffliche Eigenart der Nahrung, die verglichen mit *L. s.* neue Einrichtungen notwendig machte und andere überflüssig werden ließ.

Auch die sinnesfunktionellen und psychischen Anforderungen, die mit der Myrmecokleptie bei den wehrhaften und hochstehenden Ameisen an *A. f.* gestellt werden, haben entscheidende Veränderungen receptiver und sensibler Zentren im Sinne von Anpassungen bewirkt. So hat sich *A. f.*, vielleicht begünstigt durch den Verlust des Sehvermögens, zu einem Tasttier spezialisiert.

Eine strenge Regulation abiotischer Faktoren (Feuchtigkeit, Wärme) in Schutze des Nestes hat bei *A. f.* zu anatomischen Regressionen gegenüber freilebenden *L. s.* geführt (dünnere Körperbedeckung, analer Drüsenapparat fehlt, Rectalpapillen sind reduziert).

Eine allen Lepismatiden eigene und bei *A. f.* besonders ausgeprägte Beweglichkeit und Wendigkeit, die ihr schnelles Entweichen ermöglichen, werden a priori für das Zusammenleben mit Ameisen entscheidend gewesen sein.

Ich bin der Ansicht, daß *A. f.* ursprünglich frei lebte. Ob primär eine Verschlechterung der Lebensbedingungen allgemein, bzw. mit der räumlichen Ausbreitung verbunden, oder eine Anlockung durch Nahrungsstoffe die Veranlassung zur Teilnahme am Sozialleben der Ameisen gegeben haben mag, läßt sich nicht nachweisen. Zweifellos werden aber beide Faktoren ursächlich entscheidende Bedeutung für das Zustandekommen der Myrmecophilie bei *A. f.*, aber auch für den Anschluß an menschliche Behausungen bei *L. s.* gehabt haben. In der Phylogenese werden dann Anpassungskomplexe an die neue ökologische und biotische Umgebung entstanden sein, wie sie in der vorliegenden Arbeit aufgezeigt wurden.

### Résumé.

La cuticule mince et non pigmentée des *A. f.* s'explique par leur séjour souterrain et par l'humidité et la température égales qui règnent dans les fourmilières. Les *L. s.* sont démunis de glandes jouant un rôle dans la mue. Toutes les cellules de l'hypoderme peuvent prendre part à la mue.

Les deux espèces ont les muscles du corps et des pattes fortement développés. La coexistence des *A. f.* avec les Fourmis présuppose une grande agilité.

On trouve, en plus des glandes salivaires communes, des glandes céphaliques par paires dont les orifices séparés se trouvent dans la région maxillaire, et ceci seulement chez les *A. f.* D'après les observations, il semble qu'elles servent à nettoyer les pièces buccales et les antennes.

Seuls les *L. s.* possèdent des *corpora cardiaca*. On ne trouve de *corpora allata* chez aucune des deux espèces. Cette absence est peut-être liée à la métamorphose primitive de ces animaux. En raison des efforts



psychiques différents que doivent fournir ces animaux, leur cerveau présente des différences d'ordre anatomique et histologique. Les grappes du protocerebrum (*corpora pedunculata*), foyer des capacités psychiques, sont, bien entendu, plus fortement développées chez les *A. f.* que chez les *L. s.*

Les *A. f.* sont aveugles. Seuls les *L. s.* présentent des *lobi optici* du protocerebrum. Les *A. f.* vivant dans les cavernes des fourmilières n'ont pas besoin d'yeux.

Du fait que les *A. f.* pillent des gouttes nutritives sur les lèvres des Fourmis pendant les échanges trophallactiques, leur sens du tact est particulièrement accentué. Ceci explique le fait que le centre tactile du deutocerebrum est très développé.

Je pense qu'initialement les *A. f.* vivaient en liberté. Il n'est pas possible de savoir si c'est d'abord une détérioration des conditions de vie ou l'attrait de la nourriture qui les a amenés au commensalisme avec les Fourmis. Il n'y a pas de doute que les deux éléments y ont concouru. Il est probable que c'est dans la phylogenèse que les adaptations à leur nouveau milieu se sont produites.

### Summary.

*Atelura formicaria* possesses a thin cuticula containing no pigments which is due to the fact that it lives underground and to the equal moisture and temperature in ant-hills. *Lepisma saccharina* and *A. f.* have no skinning-glands. All cells of the hypodermis can take part in the skinning. Both animals have strongly developed body and leg muscles. Great agility is essential to *A. f.* in order to be able to live together with ants.

It is only *A. f.* that possesses besides the salivary glands, which both animals have in common, cephalic glands in pairs with separated excretory ducts near the maxilla. According to observations they seem to serve the cleaning of the parts of the mouth and the antenna.

Only *L. s.* disposes of *corpora cardiaca*. *Corpora allata* are not to be found in both animals. The primitive metamorphose of the epimetabolic insects probably renders them superfluous.

On account of different psychical efforts of the animals their brains differ in the anatomical and histological fields.

In *A. f.* the grape-like *corpora pedunculata* of the protocerebrum, where the psychical faculties are situated, are, as it is to be expected, more developed than in *L. s.*

*A. f.* is blind. Only *L. s.* possesses the *lobi optici* of the protocerebrum. *A. f.* needs no eyes in the caves of the ant hills. As *A. f.* thievishly sucks drops of food from the lips of ants feeding each other, its sense of touch is predominant. As expected the centre of the sense of touch in the deutocerebrum is accordingly developed.

My opinion is that originally *A. f.* did not depend on ants. It cannot

be found out whether in the first place the change for the worse in the conditions of life or the attraction of food caused *A. f.* to take advantage of the social life of the ants. But there is no doubt that both factors cooperated. The adaption to the new surroundings may then have come about in the course of the phylogenese.

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# THE FACTORS WHICH CAUSE COLONIES OF *APIS MELLIFERA* TO SWARM

by

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## *Introduction.*

Reproduction of colonies of the honey bee is achieved by swarming. Normally only one queen is present in each colony, but, before swarming, the colony begins to rear additional queens. The first swarm usually leaves the parental nest to found a new colony when these new queens are in the pupal stage but will sometimes do so before they reach this stage; it consists of the reigning queen and a proportion of the worker bees of the colony. One or more further swarms may leave the nest with the young queens as they emerge from the cells in which they are reared, but finally one young queen and a proportion of the worker bees are left to maintain the original colony.

Attempts to elucidate the factors which encourage swarming and to devise methods of eliminating it have received a great deal of attention in beekeeping literature and a wide variety of opinions have been expressed as to the conditions under which swarming or swarm preparations most frequently occur. Unfortunately a large proportion of these opinions appear to have no sound basis in observation, experiment or beekeeping experience. Many of them are of such a nature that their truth could only be established by large scale experiments which their authors show no evidence of having carried out, while others involve the acceptance of one particular conclusion from evidence which could be interpreted in several ways. On the other hand there are also many opinions held by beekeepers which, although not based on observations which have been published or to which reference can be made, may nevertheless be soundly based on practical experience. Such opinions must not be ignored if they are of such a nature as to be readily verifiable in beekeeping practice without liability to statistical misinterpretation.

If colonies are actually allowed to swarm, continuous observation is necessary to see whether swarming actually occurs and to avoid loss of the swarms, and for this reason investigators usually find it necessary to base their conclusions on evidence of preparations to swarm. The only readily observable characteristic of swarm preparations so far discovered, is the rearing of young queens in a colony which already has a laying queen. This, however, is also a feature of the process, known to beekeepers as 'supersedure', by which the old queen in a colony is replaced by a young one without the departure of a swarm. In supersedure, one or more young queens are reared and one of these is allowed to emerge from her cell, mate and begin laying. The remainder of the queen cells are destroyed and their occupants killed, but frequently the old queen remains alive in the colony until after the young one has begun to lay. Swarm preparations differ from those for supersedure in that no young queens are usually, if ever, allowed to emerge from their cells before the old queen, if still alive, has left the nest with the first swarm. If the weather is unsuitable for swarming the emergence of the



young queens may be delayed by the worker bees and HUBER (1792) has described how such queens are fed while still in their cells. It is generally stated (e.g. WEDMORE 1946) that preparations for supersedure can be distinguished from those for swarming by the smaller number of queens being reared. Since beekeepers are generally agreed that it is safe to assume that swarming will not take place if only a few (about one to three) queens are being reared it would appear that they have not often observed swarming under these circumstances. It seems probable, also, that the presence of a large number of queen cells (1) in a colony is a fairly safe indication that it is preparing to swarm, though the number of queen cells necessary for such an indication may vary in different colonies. There appears however, to be a wide region of intermediate behaviour within which no certain conclusion can be drawn and in which swarm preparations are difficult to distinguish from those for supersedure. This is particularly so in the early stages when the colonies have not had time to show how many queen cells they are going to produce. Since, however, experience has shown that queen rearing in colonies with laying queens during that period of the year when it occurs most frequently is far more likely to indicate preparations for swarming than for supersedure, statistical comparisons of the potential incidence of swarming at various times and under various conditions can probably be safely made from records of the incidence of queen rearing.

***Factors causing variation in the incidence of swarming at different times and indifferent places.***

The more extreme changes in environmental temperature have an obvious influence on the tendency of colonies to swarm. In temperate regions colonies swarm in summer but not in winter. Even during the summer, the emergence of swarms from their parent colonies occurs only on fine warm days, and, in persistently cold weather, swarm preparations may also be discontinued and larval or even pupal queens destroyed. The fact that swarms do not actually emerge in cold weather can be related to the difficulty which bees have in flying under such conditions, but the inhibition of swarm preparations by cold is not so easily understood; dequeened colonies will rear queens even in winter if they have eggs, or worker larvae from which to rear them.

In any one place the incidence of swarm preparations varies considerably from year to year; it also varies in the same year from one place to another (SIMPSON, 1957 a). These variations are presumably caused by minor differences in climatic conditions or by variations in the amount of pollen and nectar available in the field.

TODD & BISHOP (1941) observed that, in California, swarming was most frequent during the flowering of orange trees when nectar availability was at its greatest though supplies of pollen were scanty. NOLAN (1925) in Wyoming and MITCHENER (1947, 1948) in Manitoba also found that the maximum incidence of swarming coincided wholly or partially with the principal periods of nectar availability. MITCHENER's observations also gave a more definite indication of the effect of abundance of forage.

(1) In this paper, except where otherwise stated, queen cells are said to be present in a colony only when they contain eggs, larvae or pupae.

He divided his records into two consecutive 10 year periods and found that the proportion of the observed swarms which occurred in August was greater in the first period, when August nectar flows were an important honey source, than in the second, when they had diminished in importance because of a decrease in the amount of sweet clover in cultivation. Since, as shown by SYNGE (1947), many important nectar crops are also important sources of pollen, it is not certain whether the results of NOLAN and MITCHENER indicate that swarming tends to be associated with nectar availability or that it is encouraged by abundance of pollen.

On the other hand, ROOT (1920) considered that swarming is more frequent during light nectar flows than during strong ones, and a similar opinion was expressed by ALFONSUS & MUCK (1929). DEMUTH (1924) stated that in different parts of the United States swarming could be found to precede, coincide with, or follow after the most important periods of nectar availability. When colonies are swarming on account of overcrowding of their bees because of insufficient comb on which to expand, a good supply of nectar may relieve the congestion and stop swarming by enabling the bees to build more comb.

It seems likely, therefore, that abundance of forage tends to encourage swarming, though the effect may possibly be reversed under certain circumstances. The seasonal reduction in breeding and swarming which occurs in those tropical countries in which, during drought or monsoon periods, few forage crops are available, is presumably caused by shortage of pollen or by lack of some stimulus provided by foraging.

It is well established that in temperate climates, the occurrence of swarming is not uniformly distributed throughout the summer but is generally more frequent early than late in the summer. Thus, the 'swarming season' does not necessarily lie between particular limits of average temperature, or length of day, nor does it correspond fully with the period when nectar or pollen is most abundant. It usually ends under environmental conditions that appear to be more favourable to swarming than those under which it begins. This characteristic of the swarming season is shown by the data of TODD and BISHOP (1941), MITCHENER (1947, 1948), JEFFREE (1951) and MURRAY & JEFFREE (1955) and has been attributed (MORLAND, 1930 ; WADEY, 1943 ; CLARK, 1951 ; ARMITT, 1952) to an inherent seasonal cycle in the behaviour or physiology of colonies in which extensive breeding and growth in spring is followed by a period in which the activities of the colony are diverted from breeding, firstly to reproduction and then to accumulation of honey.

This interpretation is not supported by extensive records collected at Rothamsted of the amount of brood in colonies at different times throughout the summer. These show no evidence either that breeding declines before the season when nectar and pollen are freely available comes to an end, or that swarming occurs only after the queen of a colony has reached her maximum output of eggs. In some systems of beekeeping breeding is caused to decline early by restricting the amount of space in the hive

so that the combs become filled with honey and no space is left for brood. While this may possibly be a useful method of practical management of bees the decline in brood rearing so produced cannot be taken as indicative of the inherent behaviour pattern of the colony.

Observations of the times when queen rearing begins and ends in colonies which do not actually swarm (SIMPSON, 1957 a) and of the numbers of empty queen cell cups present in colonies throughout the summer (SIMPSON, unpublished data) have given no indication that the *tendency* of colonies to swarm diminishes in southern England before the end of July. It seems probable that the early decline in the numbers of colonies *actually swarming* is a result of elimination in the course of the season of those colonies that are capable of swarming. By the time that conditions have become most favourable to swarming most of the colonies which have not swarmed are probably those which are either unable to swarm at all or can only do so under extreme conditions, which are usually of too short a duration to allow completion of the process.

*The reasons why in the same place and at the same time some colonies swarm while others do not.*

(a) **Limitation of nest space.** — In some systems of beekeeping the number of colonies is allowed to increase by swarming in the early part of the summer so that the beekeeper can obtain honey at the end of the nectar season by destroying the extra colonies so produced or by uniting them to the remaining colonies. With these methods of management regular swarming is a necessity and it is found that it can be ensured by keeping the bees in sufficiently small hives; the capacity of straw skeps, stated by MINER (1849) and PETTIGREW (1870) to be in general use for this purpose, ranged from about 10 to 30 litres.

In other systems of beekeeping a surplus of honey is obtained by allowing a constant number of colonies to reach their full size so that the resulting increase in the proportion of bees to brood enables them more readily to produce honey in excess of their requirements. The space filled by full sized colonies has been found at Rothamsted often to be 100 to 150 litres or more.

Although many early exponents of non-swarming methods of beekeeping (e.g. COTTON, 1842 ; MINER, 1949; HUNTER, 1879; SIMMINS, 1914) claimed that swarming could be eliminated by using sufficiently large hives, experience has shown that some colonies will swarm even when care is taken to ensure that they have always more nest space than the bees can occupy. The average proportion liable to do so in southern England has been estimated to be at least 10 % (SIMPSON, 1957 a). On the other hand it is sometimes possible for the bees of colonies to be severely congested without making preparations to swarm (SIMPSON, 1957 b). Thus although colonies are very likely to swarm if they become



too big for their nest space, insufficiency of nest space is not the only factor capable of causing swarming.

It is claimed by some writers (e.g. HAMILTON, 1950 ; CUMMING & LOGAN, 1950) that swarming is encouraged by lack of space in which the queen can lay eggs rather than by insufficiency of room to accommodate adult bees. In colonies which are making swarm preparations the amount of breeding is often reduced (as recorded, for example, by TARANOV, 1947) but the scattering of honey and pollen in isolated cells throughout the brood nest, which has been considered to be the cause of this reduction of breeding, seems rather to be a consequence of it. In an observation hive it can be seen that honey and pollen are no barrier to the expansion of the brood nest of a colony, since the bees eat the pollen and transport the honey to more distant parts of the hive. In my own experiments (SIMPSON, 1957 b) three colonies which were severely overcrowded artificially, at a time when their brood nests became filled with honey, failed to swarm, while at a later date three others, which, in spite of even more severe crowding, had plenty of room for their queens to lay, did, in fact, swarm. PHILIPS (1928) states that severe contraction of the brood nest will actually reduce the tendency of colonies to swarm, and it seems possible that it may do so by preventing them from becoming large enough to swarm.

(b) **Colony size.**—The evidence of BUTLER (1954 a) that large colonies require more 'queen substance' (see next section) than small ones shows that the probability of the occurrence of queen rearing through insufficiency of queen substance must be greater with large colonies than with small ones. If queen rearing under these circumstances can lead to swarming, then swarming must be more likely to occur with large colonies than with small ones.

DEMUTH (1921) and TARANOV (1947) have claimed that in colonies which are preparing to swarm the bees tend to crowd themselves on the combs. If this crowding is an essential part of the swarming process it seems likely that its effect will be greater with large colonies than with small ones.

HOLZBERLEIN (1952) stated that it was unnecessary to look for swarm preparations in colonies which are very small in spring. GOODERHAM (1948) reported that division of colonies early in the season practically eliminated swarming. MURRAY and JEFFREE (1955), in an analysis of records of swarming collected in various parts of Scotland, failed to find any correlation between the size of colonies in spring and the incidence of queen rearing later in the season, but my own observations (unpublished) in 1956 indicate that the average size in May of colonies which produced queen cells in the course of the summer was significantly greater than the average size of colonies which did not produce them.

It is not clear from these observations whether it is the size of the colony which is important or nearness to its limit of growth. The limit of

growth of a colony occurs when its population is big enough for adult bees to be dying as fast as the queen can lay eggs. The size of a colony in this condition must be determined by the egg-laying capacity of the queen and the average length of life of the worker bees. The longevity of the workers is influenced somewhat by the amount of reserve protein present in their fat-bodies (MAURIZIO, 1950) but much more so by their degree of activity. It is very much greater in winter when they are inactive, than in the summer when they are very active, and foraging activity shortens the life of bees much more than indoor duties do (RIBBANDS, 1950). However, because little or no brood is present in colonies during the winter, the number of bees generally becomes smaller at this time than it is in the summer. By analogy with the many other organisms which reproduce themselves when they reach their limit of growth, swarming might perhaps be expected to occur in all colonies of bees when they reach full size. In fact, however, some colonies do reach full size, and continue in this state throughout the remainder of the summer, without showing any signs of swarm preparations, while others begin to make swarm preparations while they are still growing rapidly (SIMPSON, unpublished data).

GERSTUNG (1926) who assumed that colonies did, in fact, regularly swarm when they reached full size, produced a hypothetical explanation of why they should do so. He pointed out that the ratio of adult bees to larvae requiring food must be greater in a full strength colony than in a growing one, and he thought that division of labour in a colony was extremely rigid, each bee spending a fixed length of time feeding brood and each producing the same amount of brood food during the course of her life. Thus, he argued that if the bees of a growing colony could supply sufficient food for the larvae there should be a surplus of brood food in a colony which had reached its limit of growth. This surplus, GERSTUNG thought, induced the bees to make swarm preparations, in which the surplus brood food supplied the large amount of food required by the queen larvae. GERSTUNG's theory has been extended by other writers (e.g. KOCH, 1934 ; MORLAND, 1940) who have suggested that since colonies do not always swarm when they reach full size, swarming must require still greater surpluses of brood food, such as might be produced by a sudden check in brood rearing.

Gerstung's idea that under certain circumstances a colony can have a surplus of brood food appears to be partly correct. Although RÖSCH (1925, 1930) found that the division of labour in the colony was not so rigid as earlier writers had supposed (1) and that the time spent by the

(1) *Division of labour*: Ages at which bees undertake various duties are often quoted from RÖSCH's (1925) data as though they showed the existence of a rigid time schedule of occupations in normal colonies. In fact, however, they are mean figures and the behaviour of individual bees shows a wide variation. SAKAGAMI (1953) found, for example, that about a third of the bees which he observed either stopped feeding brood before they were 10 days old or continued to do so after they were 16 days old. Since all observations of work by bees within their nest (including those by PEREPELOVA, 1928, and LINDAUER, 1952) have been made on very small colo-

bees in various occupations varied according to the requirements of the colony, it has been shown (SIMPSON, 1957 b) that this adaptation is not complete. In colonies which were entirely deprived of larval brood, the pharyngeal glands of a considerable proportion of the bees showed the degree of enlargement which is associated with the feeding of brood, and when occasional larvae escaped removal, abnormally large amounts of brood food were placed in their cells, thus suggesting that brood food had accumulated in the glands of the bees.

It was found, however, that this brood food surplus did not cause the larvae to be reared as queens, nor could it be shown that it induced queen rearing by any indirect means. In fact queen rearing was not necessarily prevented by the opposite treatment in which colonies were given an excessive number of worker larvae to rear. One colony which was rearing queens continued to do so quite well even when nearly all its worker larvae appeared to be starving.

DEMUTH (1931) stated that the substitution of pupal brood for larval brood in colonies reduces rather than aggravates their tendency to swarm and that he had, in fact, used this treatment successfully as a method of swarm control in several hundred colonies. In my own experiments (SIMPSON, 1957 b) swarming did not occur when very large amounts of brood in the pupal stage were given to colonies and the adult bees were allowed to emerge there. Contrary results were obtained by PEREPELOVA (1928) who deprived some colonies of larval brood and compared them with others to which this brood had been given, and by MORLAND (1935) and BUTLER (1940) who added young bees to colonies. Since neither PEREPELOVA, MORLAND nor BUTLER mention any precautions taken to avoid over-crowding in the colonies which they used it seems possible that this factor may have led to their results. Moreover, the young bees added by MORLAND and BUTLER would not have the normal area of newly vacated cells to clean in the first few days of their life (RÖSCH, 1925 ; LINDAUER, 1952 ; SAKAGAMI, 1955) and might have caused congestion by congregating on the combs where bees were emerging.

GERSTUNG (1926) supposed that drone larvae consumed particularly large amounts of brood food and, in accordance with his theory that surplus brood food is the cause of swarming, he considered that the rearing of drones had an inhibiting or delaying effect on swarming. It has also been suggested that at certain times of year colonies automatically produce wax and that the absence of an outlet for this wax in normal beekeeping practice causes swarming. These theories have led PASCHKE (1938) and BLUMENHAGEN (1950) to devise a method of beekeeping in which the colonies are allowed some vacant space in their hives in which

ies, in which the emergence of young bees and the amount of brood to be fed usually shows large fluctuations, it might be thought that in a large colony the range of variation in the ages of bees undertaking various duties would be smaller than those which have been observed in small colonies. This seems unlikely, however, in view of the close similarity between the figures or ages when bees first began to forage, obtained by RIBRANDS (1952) from large colonies, and those obtained by other observers from small colonies.



to build drone comb (distinguished by its larger cells from the comb in which worker bees are reared). When this comb is filled with mature drone larvae it is cut out and the process repeated. No evidence seems to be available to indicate whether this method affects the incidence of swarming in any way. Since swarming is a natural process the fact that in beekeeping practice drone rearing and comb building are artificially prevented by keeping the hives full of worker combs, would seem more likely to explain why some colonies fail to swarm than why others succeed in doing so. DADANT (1890), ROOT (1920), DIGGES (1921) and HERROD-HEMPSALL (1938) all considered that swarming was encouraged by abundance of drones, but definite evidence on this point does not seem to exist.

Whilst the possibility cannot be denied that brood food surplus, or some other factor arising when colonies have a high ratio of bees to brood or when they reach their limit of growth, may have some influence on the tendency of colonies to swarm, it is clear from the foregoing evidence that none of these factors are sufficient to induce swarming by themselves. Although large colonies are more inclined to swarm than small ones the fact that some uncrowded colonies swarm whilst others do not, cannot always be explained by differences in size or in nearness to the limit of growth.

(c) **Deficiency of queen substance.**—Colonies which have their queens removed usually begin to rear new queens within a few hours. This behaviour must be directly due to absence of a queen and not to brood food surplus, since honeybee eggs take three days to hatch and, therefore, the number of larvae to be fed cannot diminish until three days after the queen has been removed. HUBER, (1792) found that the queen's influence is dependent on direct contact with the worker bees and is not transmitted by sight, scent or sound. BUTLER (1954 a, 1956, 1957 a) has shown that queen rearing is inhibited by a hormone which he has called 'queen substance' which the worker bees lick from the surface of their queen's body. He has also shown (BUTLER, 1957 b) that the cause of queen supersedure is inability of a queen to supply sufficient queen substance to prevent her colony from rearing queens.

The rearing of queens which accompanies swarm preparations presumably involves insufficiency or ineffectiveness of queen substance, but it is not yet certainly known whether this is a cause or a consequence of the swarm preparations. An observation (SIMPSON, 1957 b) that an experimentally crowded colony could swarm when the only queen cell present contained an egg suggests that queen rearing is a secondary phenomenon at least when swarming is induced by inadequacy of nest space. On the other hand swarm preparations are much less frequent with colonies with queens under two months old than with those with 1 year old queens (SIMPSON, 1957 a). Also, it is generally believed that different strains of bees differ markedly in their tendency to swarm; HERROD-HEMPSALL (1930) mentions colonies of Dutch origin which sent off repeated swarms 'until only 5 bees

and the queen are left' and TARANOV (1951) reported the existence of a Georgian strain of bees in which only 1% of the colonies swarmed. Queen and worker honeybees are both derived from the same kind of egg, the development of queen characteristics rather than worker ones being apparently dependent on the receipt by the larvae of a large quantity (HAYDAK, 1943) of food which contains a labile development regulating substance (v. RHEIN, 1933; WEAVER, 1955). Since it has been shown (KLEIN, 1904; BECKER, 1925; ZANDER, 1925) that under certain experimental conditions types intermediate between workers and queens can be obtained, it seems possible that under ordinary conditions of queen rearing some queens may be produced which are slightly lacking in the normal characteristics of queens and particularly in output of queen substance. Thus it seems possible that the capacity of queens to produce queen substance varies with their age, genetic characteristics, or conditions of rearing and that the tendency of their colonies to swarm is determined accordingly.

Neither of these hypotheses has yet been proved. If they are correct then, in any particular case when there is insufficiency of queen substance in a colony, some other factor must determine whether swarming or supersedure will result. ALFONSUS (1933) stated that supersedure occurs most frequently just before and just after the period of the year when swarming is most frequent. This suggests that supersedure may be the result of queen substance deficiency occurring when conditions are unsuitable for swarming. If so, it might be expected that small colonies would supersede ineffective queens rather than swarm with them, since the swarming of a small colony would endanger the survival both of the swarm and of the parent colony, and since a queen which was unable to inhibit a small colony from rearing queen cells would be one with a very low output of queen substance (BUTLER, 1954 a) and therefore unfit to head a daughter colony. Possibly the condition that determines that supersedure rather than swarming will occur is always that the colony's requirement of queen substance is small, either because it is a small colony or because the queen substance requirement of the individual bees is small. It seems desirable, therefore, that an attempt should be made to discover whether the queen substance requirement of worker bees is less outside the swarming season than it is during it.

#### *The circumstances under which queen cells of various types are constructed.*

The structure and appearance of queen cells is illustrated in many books on bees. In colonies making preparations to swarm or to supersede their queens the first queen cells, at least, frequently if not always begin as empty wax cups which are built on the combs with their mouths pointing downwards. Cups of this kind are nearly always present in colonies during the summer months, and the reigning queen lays eggs in them

during swarm and supersedure preparations. The cups are enlarged to full sized queen cells in the course of the growth of the larvae which hatch from the eggs.

Queens which are reared by colonies after the loss or removal of their reigning queens are necessarily produced from eggs or larvae (usually if not always, from larvae) already in cells of the type in which workers are reared. In these cases the worker cells are modified and converted into queen cells. Queen cells produced in this way are known to beekeepers as emergency cells and can readily be recognised by their structure, which is well illustrated by BUTLER (1954 b). (Queenless colonies will often construct queen cell cups also, but these are useless in the absence of a queen to lay in them). Observations in connection with experiments in 1954 (SIMPSON, 1956) showed that the production of emergency queen cells is not entirely confined to queenless colonies. When all queen cells were removed from colonies which, although not queenless, had queen cells in an advanced state, some at least of the queen cells produced thereafter were of the emergency type. Under these circumstances, moreover, emergency cells were occasionally seen which contained, not larvae, but eggs which were placed in such a position that they must have been laid after the modification of the cells had taken place; thus the presence in a colony of a larva or pupa in an emergency queen cell of typical construction does not necessarily indicate that it has been derived from an egg laid in a worker cell.

Since BUTLER (1954 a) has shown that the number of queen larvae that a colony will rear is apparently related to its queen substance requirements, thus suggesting that queen larvae can counteract the effects of queen substance deficiency, the above observations suggest that when a deficiency of queen substance develops gradually, queen rearing begins with eggs laid in cups, whereas when a large deficiency of queen substance occurs suddenly, cells containing worker larvae are modified.

### *The changes which occur in colonies during swarm preparations*

DEMUTH (1921) stated that in colonies which are making swarm preparations the bees are densely crowded on the combs. Such a condition would naturally occur in a colony which was preparing to swarm because of insufficiency of space for adult bees, but according to DEMUTH it can be observed in all colonies making swarm preparations, including those which have plenty of vacant space in the hive. He suggested that this congestion could be due to a number of factors among which was a large scale emergence of young bees.

TARANOV (1947), putting forward a theory of the cause of swarming which is an extension of that of GERSTUNG (1926), has suggested that swarm preparations are initiated by the presence in colonies of numbers of young bees which are large in proportion to the amount of brood in the



colonies. He considers that very young bees (1-3 days old) have a strong tendency to enter and remain in the brood-nest (i.e. on those parts of the combs where brood is being reared). In consequence, if the area of brood is insufficiently large, they tend to displace the older bees which are of the normal age for feeding brood. These, being unable to carry out the work to which they are physiologically suited, cluster inactively on the periphery of the brood nest. Since the metabolism of bees varies greatly with their degree of activity (KOSMIN, ALPATOV & RESNITCHENSKO, 1932) so that inactive bees necessarily crowd closely together to maintain their normal clustering temperature, TARANOV's observation bears some resemblance to that of DEMUTH.

It has been shown, however (SIMPSON, 1957 b) that an extremely large excess of young bees added to colonies does not necessarily induce obvious congestion of bees, swarming or the rearing of queens. DEMUTH and TARANOV may be right in supposing that congestion of bees on the combs is an invariably accompaniment of swarm preparations but although it may occur more readily with than without an abundance of young bees, it would appear that it does not occur unless some other factor is also present.

TARANOV and IVANOVA (1946), from observations of queens and bees on combs taken from hives and placed in a warm chamber, concluded that the worker bees (surplus nurse bees according to TARANOV, 1947), of a colony preparing to swarm become excited and pay particularly close attention to their queen, butting her with their heads, offering her food, which she does not take, and climbing on her back where they perform a peculiar 'dance'. I have not been able to observe any consistent distinction of this kind between the behaviour of colonies with and without queen cells, but it is possible that this may have been because some of the instances of queen cell production which I observed were associated with preparations for supersedure rather than for swarming. Tethering a queen on the comb in full contact with worker bees, which resulted in queen cell production if sufficiently prolonged, invariably caused the queen to be licked intensively and continuously by the workers. Some observations by MILUM (1955) suggest that the 'dance' observed by TARANOV and IVANOVA is one consisting of an oscillation of the bee's abdomen in a vertical plane. This dance is well known to observers of bee behaviour but suggestions as to its function have hitherto been lacking. MILUM states that it is usually performed by a worker bee with her front legs on some part of the body of another worker, but that when a colony is beginning to make swarm preparations, workers may perform the dance with their front legs in contact with the queen. MILUM found that bees performing this dance were mostly more than 10 days old and that it was sometimes performed by foraging bees between the dances (v. FRISCH, 1923-51) by means of which they communicate information about pollen and nectar crops. Evidence of its performance by foraging bees had previously also been obtained by ISTOMINA-TZVETKOVA (1953).

TARANOV and IVANOVA (1946) consider that the attention given to the

queen of a colony which is preparing to swarm interferes with her laying of eggs in worker cells and induces her to lay eggs in queen cells. The laying of eggs in queen cells, however, is part of the preparations for supersedure as well as of those for swarming, so that if it is induced only by the behaviour described above, the latter cannot be peculiar to swarm preparations. TARANOV (1947) stated that reduction in the queen's egg laying begins before and continues during the rearing of queens. His published figures, however, only show a reduction after the rearing of queens had begun. ALLEN (1955, 1956) observed in a colony which eventually swarmed (presumably from lack of room since it swarmed from a small observation hive) that, after queen rearing began, the queen was fed less frequently and by bees which were probably too young to be able to supply her with the protein food necessary to maintain her output of eggs. SIMPSON (1957 b) noted that the queen of an experimentally crowded colony which produced queen cells only intermittently and swarmed when the only queen cell present contained an egg, failed to show any obvious reduction in egg laying before the swarm came off. Another colony which had been given more worker brood than its bees could feed adequately appeared to give priority in feeding to the queen larvae which it possessed. These facts suggest that the reduction in egg laying which often occurs during swarm and supersedure preparations is a consequence and not a cause of the rearing of queens and that it is due to a reduction in the supply of brood food which the queen receives, either because queen larvae require a large amount of brood food or because the amount of brood food which a colony gives to its queen is related to the amount of queen substance which she supplies. If so it seems possible that when, during supersedure, the old queen disappears after the young one has begun to lay this may be because the old queen, producing less queen substance than the young one, receives little brood food and dies from shortage of protein. MAURIZIO (1946, 1950, 1954) has shown that the life of worker bees is extended by an excess of protein in their diet, so it seems possible that the long lives of queens are dependent on the receipt of much protein.

TARANOV (1947) concluded that, as swarm preparations advance, nurse bees become displaced from the brood nest in ever increasing numbers and become differentiated from the colony as 'swarm bees', i.e. the bees which form the swarm when it departs. The latter part of this conception is an attractive one, since it explains what determines which bees will leave with the swarm. It is in agreement with TARANOV's own observations and those of BUTLER (1940) that the youngest bees capable of flying contribute the greatest proportion of their numbers to the swarm. As evidence in support of this 'swarm bee' hypothesis, TARANOV noted that most of the bees which left the colony with a swarm had previously been located on the outer combs or in parts of the hive not filled with comb, while few of them came from the areas with larval brood. He also stated that the numbers of bees foraging immediately before and after the

emergence of a swarm were similar, thus suggesting that the same bees were foraging, few, if any, having departed with the swarm. Confirmation of this conclusion was obtained in connection with two colonies which swarmed after experimental crowding (SIMPSON, 1957 b). In each case it was estimated that at least 90 % of the bees in the colony came off in the swarm, yet with one colony 6 previously marked foragers were found in the swarm and 14 in the parent colony and with the other, 14 were in the swarm and 27 in the parent colony. These results are significant ( $P < 0.001$ ), even when allowance is made for substantial errors in the estimates of the proportion of bees leaving with the swarms, and they show that the swarms contained a smaller proportion of the foragers than of the other bees in the colonies.

TARANOV also attempted to produce more conclusive evidence of the differentiation of 'swarm bees'. He marked 200-500 bees in each of three swarms and returned them to their parent colonies. The latter were later examined when the swarms had emerged for a second time and it was found that only about 10 % of the marked bees had remained. Unfortunately, TARANOV does not state what proportion of all the bees in the colonies left with the second swarms, so it is impossible to tell from the figures given whether or not this distribution could have been produced merely by random mixing. Elsewhere in his paper he mentions cases where only 20 % of the bees remained in colonies after swarming, and a case is noted above where it appeared that less than 10 % remained. The figures given by BUTLER (1940), however, as well as general experience, suggest that the average figure is considerably higher. TARANOV's conclusion may, therefore, be sound though it might be difficult to obtain a decisive result by repeating his experiment.

It would appear from the foregoing evidence that much remains to be learned about the processes which occur in colonies which are preparing to swarm. It seems possible that congestion of bees in or around the brood nest always plays a part and that the departure of a swarm relieves this congestion, perhaps by removing 'swarm bees'. The cause of this congestion when it occurs in a colony which is not lacking in space for bees is, however, obscure.

### *The factors responsible for the actual emergence of swarms from colonies.*

It is generally believed by beekeepers that the presence of queen cells, particularly those containing queens in the pupal stage, in colonies making preparations to swarm, greatly increases the likelihood that swarming will actually take place. Because of this belief, when colonies are found to be making what are believed to be swarm preparations, queen cells are removed as a matter of routine by beekeepers if no other treatment is thought necessary. It is also considered desirable to reduce the number



of queen cells in a queenless colony to one, since it is thought that swarming with the first young queen which emerges from her cell is more likely to occur if other queen cells are present. Although it is not entirely unknown for swarms to emerge when queen cells have been removed and no more have yet been produced, it seems to be generally agreed among beekeepers that this is not a common occurrence. However, since, when well advanced queen cells are removed from a colony, new ones are often produced by modification of cells containing worker larvae, it would appear that the length of time during which a colony under these conditions remains without queen cells is generally short, so that the probability that a swarm will emerge while no queen cells are present is small. Thus the rarity of the emergence of reproductive swarms from colonies without queen cells may be no indication that the presence of queen cells encourages colonies to swarm.

It is also stated (for example by PHILLIPS, 1928) that removal of queen cells when they are still in the early stages will often stop colonies from making further preparations to swarm. It is unlikely, however, that satisfactory evidence that this is so exists since colonies frequently destroy queen cells (even those containing larvae) of their own accord and may then make no further preparations to swarm in that season (SIMPSON, 1957 b).

Little seems to be known about the stimulus immediately responsible for the emergence of swarms. As already noted, observations by DEMUTH and TARANOV suggest that swarm preparations are invariably accompanied by congestion of bees on the combs even when there is plenty of vacant space filled with comb in the hive. If this is so, it would appear that the factors which cause swarming in colonies which have unlimited room do so by altering the behaviour of the bees in such a way that they tend to pack themselves closely on the combs. Under these conditions a sudden increase in the activity of the bees might produce a rise in temperature sufficient to cause them to leave their nest. However, an attempt (SIMPSON, 1956) to stimulate the emergence of a swarm from a colony artificially showed that this explanation is, at least, incomplete. By closing the entrance of the hive, disturbing the bees severely with smoke and then opening the entrance again it was found possible to induce a large proportion of the colony to come out, but the behaviour of the bees differed from that which is shown by an emerging swarm. Instead of flying as soon as they came out of the hive, they ran over the outside of the hive and formed a cluster there.

HUBER (1792) observed that the queen and workers appear to become very excited immediately before the emergence of a swarm. He thought that the excitement of the workers was caused by the behaviour of the queen. A queen is certainly necessary for the complete process of swarming since a swarm without a queen usually soon returns to the parent colony. It is doubtful, however, whether the queen is responsible for initiating the emergence of a swarm. PHILLIPS (1928) states that a swarm may leave the hive even if the queen is in a cage, and many obser-

vers, including TARANOV & IVANOVA (1946) and ALLEN (1956), have noted that the queen does not lead the swarm out of the hive but often appears to be pushed out by the worker bees. On the other hand ALLEN's observations showed that the queen began to make the peculiar sound known as 'piping' when the young queens in their cells were still in the pupal stage and incapable of responding to it, whereas the worker bees apparently did respond by remaining motionless when the queen was piping. 'Piping' by queens is associated with the presence of queen cells during swarm preparations but not during those for supersedure. Thus it seems possible that the piping (induced according to WOODS, 1956 by the effect on the queen of the smell of queen cells) serves to excite the worker bees in such a way that they become ready to swarm.

LINDAUER (1955) has shown that the signal which leads to the emergence of a swarm is given by a dance performed by some of the bees. He has found that the bees which search for a new nest site before the colony swarms are ones which have previously been foraging, and he considers that these bees are diverted to their new occupation by finding insufficient room in the hive to receive their loads of nectar. The latter conclusion seems unlikely to be correct since swarming is not necessarily associated with lack of space for storage of food (SIMPSON, 1957 b). The operative factor might, however, be cessation of nectar acceptance by bees in the hive rather than lack of storage room since, as first shown by DOOLITTLE (1901), foragers do not put nectar directly in the cells but transfer it to other bees.

In *Apis dorsata* and *A. florea*, migration of the whole colony occurs in addition to reproductive swarming. Migration appears to occur when environmental conditions are unfavourable, and in mountainous regions there may be a regular movement of colonies downwards in cool seasons and upwards in hot seasons (ROEPKE, 1930; BUTLER, 1954 b). Reproductive swarming, at least in *A. dorsata*, seems to be most frequent when plenty of forage is available (ROEPKE, 1930). Regular migration does not occur with *A. indica*, but an irregular type of migration, known to Indian and Ceylonese beekeepers as 'absconding' frequently occurs during periods of dearth caused by drought or monsoon, particularly if the colony is disturbed. With this species also, reproductive swarming most readily occurs under good foraging conditions (RHAMAN, 1945; BUTLER, 1954 b). In general the behaviour of *A. mellifera* appears to differ from that of the foregoing species in that instead of migrating it makes special preparations for winter, including enlargement of the worker bees' fat-bodies (LOTMAR, 1939; MAURIZIO, 1954), but it also shows a vestigial tendency to migrate in the form of behaviour known to beekeepers as 'hunger swarming', which is sometimes shown by colonies which are short of food. A commoner and probably related form of behaviour is shown when a colony leaves a hive which has become unsuitable for habitation. The departure of swarms from the position (usually on a tree or bush) where they first settle after leaving the parent colonies, and the tendency of swarms to

depart if put into peculiar structures such as observation hives, are probably also due to rejection of positions which do not possess the characteristics which attract swarms to nest sites; some information about these characteristics has been obtained by LINDAUER (1951, 1953, 1955).

It seems possible that in all forms of swarming or migration the factor which causes the bees to leave their nest places is some form of 'dissatisfaction' with their environmental conditions, although in the case of reproductive swarming this 'dissatisfaction' must either be relieved by the departure of only a proportion of the bees of the colony or be present only in the 'swarm bees'.

### *Summary.*

1. The rearing of young queens by colonies which already possess laying queens is characteristic of two pieces of behaviour known respectively as 'swarming', which is the method by which colony reproduction occurs, and 'supersedure', by which the reigning queen of a colony can be replaced without the occurrence of swarming.

2. The incidence of swarming among colonies of bees varies from year to year and place to place. Swarming is encouraged by warm weather and abundance of forage but otherwise the effect of environmental factors on its incidence is obscure.

3. Swarming is more frequent early than late in the summer but the impression thus given that in the course of the summer some change occurs in the condition of the colonies may well be an illusion produced by exhaustion of the supply of colonies capable of swarming. The decline in brood rearing which some observers have found in the middle of the summer is probably a consequence of certain systems of beekeeping since it does not occur naturally in colonies which have unrestricted nest space.

4. Colonies readily swarm if they become too big for their nest space but many will also swarm when not restricted in this way.

5. Large colonies are more liable to swarm than small ones but there appears to be little evidence that the tendency of colonies to swarm is increased by approach to their limit of growth.

6. Increase in the amount of brood food available for larvae, such as may occur when a colony reaches full size or when its brood rearing declines, does not cause swarming.

7. The rearing of queens by a queenless colony is due to absence of inhibition by 'queen substance' and not to surplus brood food.

8. Queen supersedure is induced by inability of a queen to produce enough queen substance to inhibit her colony from rearing queens, but it is uncertain whether swarming also can be induced by such a deficiency, or whether the queen rearing which occurs during swarm preparations is not always a secondary phenomenon occurring as part of a process initiated by other factors.

9. From the little evidence available it seems possible that queen



substance deficiency induces swarming in large colonies when the environmental conditions are favourable to swarming and supersedure in small colonies or in large ones during unfavourable environmental conditions.

10. Queen cells of the 'emergency' type which are produced by queenless colonies can also occur in the presence of a laying queen under certain circumstances, possibly those in which a large queen substance deficiency occurs suddenly.

11. In uncrowded colonies which are making swarm preparations there may be a tendency for the worker bees to congregate closely on the combs thus producing conditions similar to those which occur when a colony is induced to swarm by insufficiency of nest space.

12. There is some evidence that during swarm preparations there is a change in the behaviour of the worker bees towards their queen as a result of which she lays fewer eggs.

13. The bees which form a swarm may possibly become differentiated from the others in the colony before the swarm emerges.

14. Satisfactory evidence seems to be lacking as to whether the emergence of a swarm is encouraged by the presence of occupied queen cells in the colony.

15. The emergence of a swarm is stimulated by a dance performed by some of the worker bees. It is not induced simply by overheating resulting from a disturbance amongst closely packed bees, nor is it initiated by the queen of the colony, although the queen's 'piping' may perhaps play a part in making the worker bees ready to swarm.

16. *Apis mellifera* differs from *A. dorsata* and *A. florea* and also to some extent from *A. indica* in that special preparations are made for winter and the colonies do not migrate when conditions become unfavourable to their activity.

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POLYETHISM IN WORKERS OF THE ANT MYRMICA

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I. — INTRODUCTION

This work was undertaken in the course of an investigation into the factors controlling dormancy in female larvae of the ant *Myrmica*, carried out between the years 1951 and 1954. The author is indebted to the Carnegie Trust for the Universities of Scotland for a grant enabling this work to be undertaken; also to Professor C. M. Yonge and members of the staff of the Zoology Department of the University of Glasgow; in particular to Dr. J. W. H. LAWSON, Dr. W. RUSSELL HUNTER and Mr. D. A. MUIR for their advice and guidance; finally to Mrs. A. D. BRIAN, and to Mr. M. V. BRIAN (now of the Nature Conservancy, Dorset) without whose continued encouragement and advice this work would not have been undertaken.

The material used in this investigation comprised colonies of the following species: *Myrmica laevinodis* Nyl., *Myrmica scabrinodis* Nyl., and *Myrmica rubra* (L) as divided into *M. rubra microgyna* and *M. rubra macrogyna* by BRIAN and BRIAN (1949).

All colonies of ants used were collected in the counties of LANARK, DUNBARTON, STIRLING and AYR in the West of Scotland.

The significance of this section of the investigation and its relationship to other work which has been completed is as follows. Experiments on the induction of dormancy in female myrmicine larvae (carried out initially by BRIAN (unpublished) and subsequently by the present author) have shown that the physiological "condition" of the workers is important. Worker "condition" has been defined by BRIAN (1954) who has separated workers into three sequential seasonal categories (vernal, aestival and serotinal) which can be compared with a similar series of physiological "conditions" observed in the laboratory. The present author has used the term prevernal to describe

another seasonal worker condition. For larval growth, the 26 week summer in the West of Scotland is equivalent to a 13 week season at 25°C in the laboratory (BRIAN, 1954). The four terms used can therefore be defined as follows:

*Prevernal*. — Workers collected in the field in March and early April. Workers during the first three weeks of incubation at 25°C after hibernation at 10°C.

*Vernal*. — Workers in the field in May, and workers between four and six weeks after the start of incubation at 25°C.

*Aestival*. — Workers in the field in July, and workers between seven and nine weeks after the start of incubation at 25°C.

*Serotinal*. — Workers in the field in September, and workers between ten and twelve weeks after the start of incubation at 25°C.

The present work examines the origin of these differences of "condition", and the mechanisms by which they affect the brood rearing capacity of workers at different seasons.

EHRRARDT (1931), working on *Myrmica rubra* (the taxonomy of this and other related species in Britain has recently been discussed by BRIAN and BRIAN, 1949) showed that the behaviour of individual workers differed and that there was apparent change in the behaviour of individual workers with age. The ethological changes she describes show that the young workers are associated for long periods with the brood mass but, as they become older, they show increasingly a tendency to stand near the brood mass not, apparently, doing anything in particular. Finally the workers become foragers and spend little time with the brood mass. These observations showing ageing accompanied by worker polyethism in a monomorphic species of ant have not hitherto been pursued. In addition to the classical examples of polyethism described in highly polymorphic genera (examples are quoted in WHEELER, 1910), differences in worker behaviour within the same caste have been demonstrated by CHEN (1937). Investigation of these conditions in colonies of characteristically monomorphic genera, as WILSON (1954) considers *Myrmica*, is desirable. In particular, both differential worker behaviour and the possible polymorphism associated with workers of differing ethal types (workers showing behaviour differences) require study. Both these problems have been investigated and the results are described in the present papers.

## 2. — PRELIMINARY EXPERIMENTS WITH COLONY FRAGMENTS

On the basis of Ehrhardt's observations (1931) it appeared that ageing of the ant colony could cause increased worker activity (foraging). Such increased activity in senescent ants could be solely responsible for the different brood rearing capacities of worker colony fragments of different seasonal ages. Two experiments were therefore undertaken as follows.

EXPERIMENT I. — The relative oxygen consumption of colony fragments of varying seasonal ages was measured by modified Barcroft respirometers. The experiment was unsuccessful because the rate of oxygen consumption of the worker group as a whole, was masked by the oxygen consumption of individual workers which were, sporadically, very active. Not more than 5 % of the workers were active at any one time. No statistical differences could be detected between the age groups.

EXPERIMENT II. — The relative locomotor activity of colony fragments of varying seasonal ages was measured by means of an actograph (CHAUVIN, 1947). Individual workers were again responsible for most of the



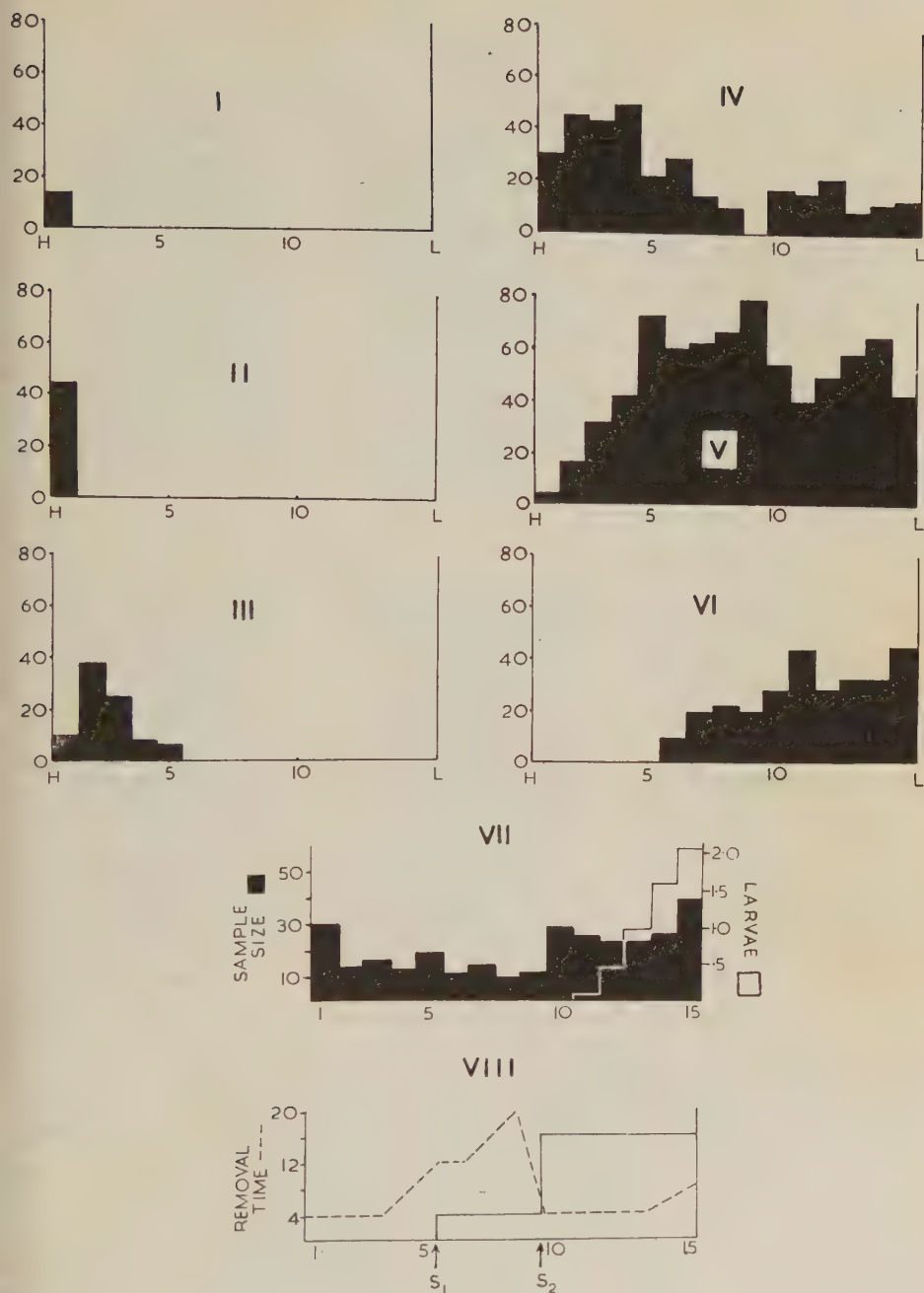


FIG. 1. — Shows in parts I-VI the percentage of each activity sample composed of workers of the appropriate melanic group (I-VI). The abscissa shows activity samples. (H-high activity, L-low activity). The ordinate axis shows percentage composition. Part VII shows the total sample size in black, and the occurrence of larvæ in outline, as plotted against activity sample. Part VIII shows the time of removal of each activity sample in minutes, and the periods of artificial stimulation (first,  $S_1$ ; second,  $S_2$ ) both plotted against activity sample.

activity recorded, and these few, highly active workers masked any differential activity of the residual workers tending the brood. As a result, these experiments were abandoned, since it was necessary to measure the difference in locomotor activity between the individual workers of separate colony fragments; and determine both the cause of this difference, and whether it had any effect on brood rearing.

### 3. — CONDITIONS IN A COLONY OF *MYRMICA SCABRINODIS*

#### A. — *Worker segregation.*

The workers of a medium sized colony of *M. scabrinodis* were separated into activity samples in the following way. The colony (collected in the field in early October, 1953, and therefore in a late serotinal condition) was cultured for one week at 25°C without food. It is probable that the colony was short of food as a result. (Some workers may be said to have been hungry.) The glass cover of the plaster nest (BRIAN, 1951 *a*) was then removed from the food chambers and the workers were collected as they emerged. The food chambers are furthest from the brood chamber. Samples were removed every ten minutes, but the number of workers in each sample could not be regulated accurately. The time required for the removal of a sample of fifteen to twenty workers was, at first, four minutes, but rapidly increased. Similarly the sample size decreased. In order to keep the time of sampling, the time for the removal of the sample, and the size of the sample as constant as possible, the nest was stimulated by blowing. Blowing gently into the dry chamber of the nests once every thirty seconds facilitated the separation of activity samples 6 to 9.

After the removal of sample 9 it was necessary to increase the amount of stimulation of the workers in order to maintain a constant sample size and time for removal. The nest was stimulated by blowing gently into it once every ten seconds. The necessity for stimulation may not have introduced a completely new factor into the worker separation, since it is impossible to say to what extent the workers were stimulated initially by vibration of the nest when the glass cover was removed or air displacements, etc., at that time. The levels of stimulation to which the colony was subjected during its separation have not been assessed relatively.

All two hundred and ninety one surviving workers were included in fifteen activity samples, the last of which, totalling about forty workers, comprised the residual workers and larvae from the brood chamber. During the removal of the eleventh sample, workers carrying larvae were first detected. The results of the separation are shown as histograms in figs. 1.VII and VIII. In fig. 1.VII, the black histogram shows the worker numbers in each activity sample, and the outlined histogram the approximate larval numbers. In fig. 1.VIII the broken line shows the time in minutes for the removal of each sample, and the continuous line shows

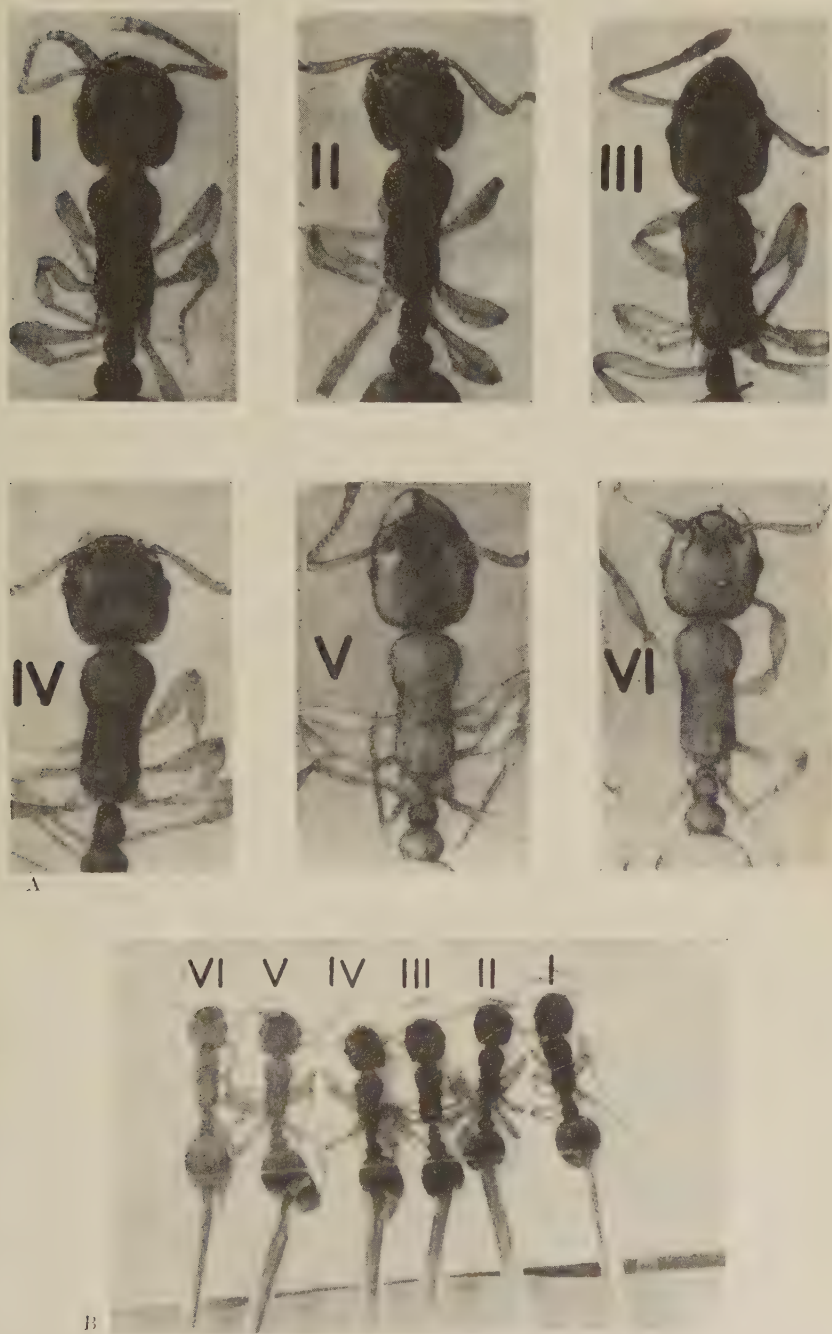


FIG. 2 A et B. — Six melanic worker types. The antennæ and legs do not show the range of cuticular melanisation shown by the cephalic and thoracic cuticle.



the points of increased stimulation. ( $S_1$  = one puff every 30 seconds;  $S_2$  = one puff every 10 seconds.)

It should be noted that at least three separate factors have been used to achieve this worker segregation. These are:

A. Hunger, with possible resultant high locomotor activity in search of food. — B. Inherent high locomotor activity as opposed to inherent low locomotor activity. — C. High reactivity (sensitivity to stimulation) as opposed to low reactivity.

If the initial separation is by a hunger stimulus, ideally one should collect over a period of days those individuals which become hungry, if the basis of separation is to be strictly uniform throughout. The time taken to achieve such a separation would defeat the purposes of the investigation, so the process is speeded up by applying stimulation. But the situation is further complicated. It is convenient, at this point, to consider the separation as one of varying grades of locomotor activity. The assumption that hunger is partially responsible for the worker separation implies that "foragers" exist among the workers. The use of the term "forager" may be descriptive and imply ethological purposefulness accompanied by high locomotor activity. It is convenient to avoid the use of the term forager in this particular sense, since all workers with high locomotor activity need not, in theory, be foragers. The association of high locomotor activity with a tendency on the part of the worker to wander away from the brood mass would increase automatically the chance probability of the worker meeting suitable food. It is nevertheless convenient to use the term "forager" for workers with high locomotor activity. It should, however, be clearly understood that no purposefulness is implied by this phrase. This question is referred to subsequently (p. 124).

The application of stimuli which speed up the process of separation, introduces another factor. It may be assumed that after the first stimulus ( $S_1$ ) has been applied to the nest (if indeed the nest has not already been accidentally stimulated by previous removals of worker samples), worker separation is largely on the basis of reactivity or sensitivity. The degree of homology between this separation and that based on activity is unknown, and has not been estimated.

A further separation of the fifteen samples was then undertaken. Each sample was subdivided, after careful examination of the individual workers, into six melanic (1) groups designated I, II, III, IV, V and VI. Photomicrographs of the six melanic groups are shown in figure 2 A. The percentage composition of each sample belonging to the appropriate melanic group is shown in figure 1. The most highly melanised individuals were those of group I, and the most lightly melanised those of group VI.

(1) The use of the word melanic denotes only a darkening of the cuticle. No biochemical tests have been made to determine whether this change is due to the pigment melanin as defined by Lison (1936). Subsequent research on this pigment has been reviewed by Fox (1953).

From figure 1, it can be seen that the most highly melanised individuals, i.e. groups I and II, were confined to activity sample 1. Group III reached a maximum in sample 2, group IV in sample 4, and group V in sample 9. The most lightly melanised individuals (group VI) reached a maximum in sample 15. This segregation on the basis of melanisation shows that a series of visibly distinguishable activity groups has been separated. The melanic differences between adjacent groups were small. The separation was only accomplished by the comparison of individual workers under a spotlight. Relative differences are shown in figure 2 B. It is apparent that there are three distinct major melanic types (groups I+II; III+IV; and V+VI), each of which has been 'subdivided' by less obvious melanic differences to form six melanic groups. Only the separation of workers in groups I and II was difficult and, on a solely melanic basis, of doubtful validity. The small numbers of workers of groups I, II and III facilitated experimentation on this point. Those workers of groups I, II, III, IV and V, which had been removed in activity sample 1, were cultured together for a week at room temperature (22°C to 18°C) on a full food diet. The separation of the workers in these groups was then repeated, without stimulation, and the individual workers were placed in numbered tubes as they emerged from the nest. This was repeated three times on three successive days. The results showed a high degree of correspondence, but the form of the experiment was not amenable to statistical analysis. A typical result is therefore shown in table I.

TABLE I. — ORDER OF EMERGENCE FROM NEST.

MELANIC GROUPS.										
I	XXX	X								
II		XX	XXX	XXX	XXX	X	X			
III						X	X		X	
IV							X	X	X	XXX
V										XX
ORDER OF EMERGENCE	3	6	9	12	15	18	21	24	27	30

There appeared to be sufficient differential activity to justify the separation of these highly locomotor workers into the groups I, II and III. It is clear then that the difference between groups I and II and between groups III and IV, though small, is nevertheless real.

The composition of the above nest is shown in table II.

TABLE II.

MELANIC GROUP.	TOTAL NUMBER OF WORKERS.	% OF TOTAL POPULATION.
I	4	1.3
II	13	4.4
III	14	4.8
		} 10.5
IV	62	21.3
V	133	45.7
VI	65	22.3
		} 89.3

From table II it is apparent that melanic group V is the largest and that the adjacent groups IV and VI are next in size to it. Together these three groups represent 89.3 % of the population. The highly active workers represent only 10.5 % of the total population, which is therefore numerically dominated by groups associated with the brood mass.

It was apparent, from observation, that melanic group VI was composed of workers produced from eggs laid during the preceding summer (1953), (i. e. from non-dormant larvae). It was equally apparent that melanic group V was composed of workers which had been produced in the spring of 1953 from overwintered larvae. The implication of a progressive melanisation occurring throughout the life of the worker was noted. Melanic groups I to IV were therefore all composed of workers which had been adult for more than one year, and further, by implication, those in melanic groups I and II were considerably older.

The following experiment (3) was then carried out. Fifteen workers of each of the three melanic groups IV, V and VI, were cultured with five larvae at 25°C on a full food diet. After two months the surviving workers were examined. After removal of the new workers produced from the larvae in each culture, it was still possible to distinguish between the workers of the three original melanic types. There were few survivors from culture IV, but these were darker than other members of melanic group IV which had not been cultured at 25°C but kept at 10°C for sometime previously. Similarly it was possible to differentiate between workers of the same original melanic groups (either V or VI) which had been reared, some at 25°C and some at 10°C. It can be concluded that melanisation occurs more rapidly at 25°C than at 10°C, and that the differences between the melanic groups are partially attributable to different ages. While this is true of the difference between groups V and VI (which represent respectively the overwintered brood and non-dormant brood of one season), the age relationships of the other melanic groups are obscure. This is discussed subsequently.

Visible differentiation of workers of melanic groups II, IV and VI was possible, even in dim light, and these groups were therefore used in sub-



sequent experiments and observations. As previously stated, the colony was collected in early October. The subsequent separation, which has been described in detail, was carried out over a period of eight days, during which time the colony was kept at room temperature ( $18^{\circ}\text{C}$ — $23^{\circ}\text{C}$ ). When the separation was complete, the six melanic components of each activity sample had been separated from each other and were being cultured in isolation on a full diet. The cultures were then left for one more week at room temperature and then transferred to a thermostatically controlled cold room at  $10^{\circ}\text{C}$ . Here they remained for a period of twenty-one days. They were then removed after this comparatively short chilling, and incubated at  $25^{\circ}\text{C}$  on full diet. The course of events can, as a result, be shown diagrammatically as in table III.

TABLE III

WEEKS.	1	2	3	4	5	6	7	8
Temperatures.	$25^{\circ}\text{C}$	$18\text{--}23^{\circ}\text{C}$	$18\text{--}23^{\circ}\text{C}$	$10^{\circ}\text{C}$	$10^{\circ}\text{C}$	$10^{\circ}\text{C}$	$25^{\circ}\text{C}$	$25^{\circ}\text{C}$
	← Colony Separation →		← Isolated worker Components →					

Such a perfunctory hibernation period has been successful for the overwintering of workers and queens. For the successful vernalisation of larvae this period may, however, be quite inadequate (BRIAN, 1954).

### B. — Worker activity and job preference.

The results contained in this section are derived from one experiment (4) carried out on the post-hibernated *M. scabrinodis* nest. Other observations on workers from this nest have confirmed the results enumerated below.

Experiment 4 began six weeks after the workers had been segregated, and was designed as follows. Eight plaster of Paris nests (BRIAN, 1951 a) were used, each with a full food supply. Conditions were standardised as far as possible. Each nest contained six workers and ten larvae. The larval growth is considered in Section C below. The worker composition of each colony fragment is shown in table IV.

Such an experimental design will reveal both lasting differences of activity within and between melanic groups, and also the effects of numerical variation of worker number.

At each observation, careful removal of the cover from the nest revealed both the position and occupation of the workers. During each census fifteen observations were made on each nest. The first activity census lasted six days, and the remaining two each lasted three days. Only

some of the resulting data are described, namely those from which interesting sociological conclusions can be drawn or from which statistically significant differences have been obtained after F tests of the partitioning of variance (SNEDECOR, 1946). Results on worker activity are considered in three sections:

TABLE IV. — WORKER COMPOSITION OF SYNTHETIC COLONY FRAGMENTS.

Where: a = Melanic group of workers concerned. — b = Number of workers belonging to that melanic group. — c = Activity sample in which the individual workers were segregated.

	FRAGMENT 1.	FRAGMENT 3.	FRAGMENT 5.	FRAGMENT 7.
	a b c	a b c	a b c	a b c
WORKERS OF MELANIC group VI from activity samples 11 or 12.	VI 6 15	VI 4 15	VI 4 14 & 15	VI 4 14 & 15
		IV 2 15		IV 1 15
			II 2 1	II 1 1
	FRAGMENT 2.	FRAGMENT 4.	FRAGMENT 6.	FRAGMENT 8.
	a b c	a b c	a b c	a b c
WORKERS OF MELANIC group VI from activity samples 14 or 15.	VI 6 11 & 12	VI 4 11	VI 4 11 & 12	VI 4 11
		IV 2 15		IV 1 15
			II 2 1	II 1 1

a) TOTAL NEST ACTIVITY.

These results are tabulated in tables V.A-E. These show the numbers of workers at each census engaged in three possible "occupations" or "jobs" similar to those described by EHRHARDT (1931), namely:

—Workers on the brood mass (i.e. workers in contact with a larva).

—Workers near the brood mass (i.e. workers which by head or antennal movement would come in contact with a larva, or a worker on a larva, or another worker which was in such a position).

—Workers which were not near the brood mass.

In this last category, it was possible to distinguish between workers in the food chambers or the dry chambers, and workers in the wet chamber. Similarly, it was possible to distinguish a fourth category of behaviour, namely that of workers which, by pulling on the cotton wool or biting the plaster of Paris, were attempting to build a nest. Data on the incidence of this behaviour is given after table V.E.

Statistical analyses of the results presented in tables V.A-E, show that the differences between certain pairs of nests (1+2; 3+4; 5+6; 7+8) are significant: i.—The number of workers on top of the larvae in nests 5+6 is low (table V.A).—ii.—The number of workers near the larvae shows no significant difference (table V.B).—iii.—The total number of workers on and near the larvae (i+ii) shows striking variation (table V.C). Nests 1+2 and 3+4 have uniformly high values, but the values for nests 7+8 are lower. Values for nests 5+6 are lowest of all.—iv.—Corresponding to the values noted in iii above, the number of workers away from the brood mass shows an inverse situation, where nests 5+6 have the highest values, and nests 1+2 and 3+4 the lowest (table V.D).—v.—The total length of all worker trips varies between the nests as does iv above (table V.E).—vi.—The occurrence of attempted nest building is confined to two nests. (Data listed below table V.E.)

It is apparent that variation of the melanic group composition of synthetic colonies causes differential activity and behaviour.

**Tables V.A-E.**—These five tables show the variation in activity and worker occupation in the eight nests during the three census periods, each of three days duration. The subdivision of the table into four columns facilitates comparison of the results between colony fragments of differing melanic group composition. The difference between the members of each pair shown in any one column is the intra-melanic difference of activity sample (p. 106). No statistical differences are attributable to this later level of worker segregation in these five tables.

TABLE V.A. — TOTAL NUMBER OF WORKERS ON THE BROOD MASS.

	NESTS.							
	1	2	3	4	5	6	7	8
Census 1.	69	59	65	49	46	48	61	61
Census 2.	74	64	70	73	53	54	68	70
Census 3.	66	62	70	80	54	49	66	63



TABLE V.B. — TOTAL NUMBER OF WORKERS NEAR BROOD MASS.

	NESTS.							
	1	2	3	4	5	6	7	8
Census 1.	18	24	15	11	20	12	11	20
Census 2.	13	22	14	13	8	21	7	9
Census 3.	17	23	13	5	10	23	9	19

TABLE V.C. — TOTAL NUMBERS OF WORKERS ON OR NEAR BROOD MASS.

	NESTS.							
	1	2	3	4	5	6	7	8
Census 1.	87	83	80	60	66	60	72	81
Census 2.	87	86	84	86	61	75	75	79
Census 3.	83	85	83	85	64	72	75	82

TABLE V.D. — TOTAL NUMBER OF WORKERS AWAY FROM BROOD MASS.

	NESTS.							
	1	2	3	4	5	6	7	8
Census 1.	3	7	10	13	24	30	18	9
Census 2.	3	4	6	1	29	15	14	11
Census 3.	7	5	7	4	26	18	14	8

TABLE V.E. — TOTAL LENGTH OF WORKER TRIPS.

	NESTS.							
	1	2	3	4	5	6	7	8
Census 1.	6.5	19.5	17.5	3.10	48.5	74.5	40.5	30.5
Census 2.	8.0	6.5	11.5	5.0	107.5	35.5	44.5	34.5
Census 3.	14.0	8.5	18.0	7.5	68.5	43.0	41.0	26.5

In table V. E. distance from the brood mass is shown in arbitrary units, where for instance:

5.0 = Worker in food chamber (maximal value).

2.5 = Worker at entrance to wet chamber.

*Number of workers engaged in attempted nest construction:* Attempted nest construction was noted in nests 4 and 7. In nest 4 the number of workers so occupied during censuses 1, 2 and 3 respectively was 7, 3 and 1. In nest 7 during censuses 1, 2 and 3 respectively it was 0, 1 and 1.

#### b) VARIATION WITHIN MELANIC GROUPS.

—The results discussed in this section are given in table VI, and in the data enumerated immediately after table VI. These have been simplified for ease of comprehension and show only the average values concerned.

*Melanic group VI.*

1.—*Workers on the brood mass.*—Analysis of the number of workers of group VI on the brood mass (data A) shows significant differences between: i.—the numerical nest compositions.—ii. the original activity samples.—iii.—the three census periods.

(i) Adjustment of worker numbers to a uniform value in this analysis shows (data B) that nests 1+2 [which, before this adjustment have a significantly higher number of workers on the brood mass compared with the other nests] have, when adjusted, a significantly lower number of workers on the brood. It is unreasonable to suppose that six workers cannot get on top of ten larvae. Therefore, while more workers were standing on the larvae when six workers were present, this increase was not proportional to the higher number of workers. Among the possible interpretations of this result are: a.—Workers of melanic group VI normally stand on the larvae when workers of other melanic groups are present, but will do otherwise if no other melanic groups are present. (Teleologically they have a preference for one occupation.) b.—Workers of melanic group VI show a range of behaviour and by themselves may stand on the brood or do otherwise. When workers of other melanic groups are present there is competition for jobs, resulting in group VI workers being forced onto the brood mass.

These two possibilities are not mutually exclusive and both may be operative in different populations.

(ii) Workers of melanic group VI from activity samples 10+11 spend less time on the brood than workers of melanic group VI from activity samples 14+15. This is in agreement with the results derived from the initial segregation and it is concluded that differences within the melanic groups, between workers of relatively low activity as opposed to workers of relatively high activity, are permanent and not ephemeral.

(iii) The significance attached to the differences between censuses is obscure, but probably reflects changes in the size of the brood mass with increasing larval growth.

2.—*Workers near the brood mass.*—Differences exist in the numbers of workers of group VI near the brood mass (data C, adjusted for worker number), and occur as follows: i.—between four melanic group compositions.—ii.—between the two activity samples of melanic group VI.

(i) The higher values in nests 1+2 (even when adjusted) correspond to the lower values for workers on the brood noted in (i) above. Thus, in the absence of workers of other melanic groups there is a significant increase in the numbers of workers of group VI standing near the brood.

(ii) Relatively high activity workers of melanic group VI from samples 10+11, differ ethologically from the relatively low activity group VI workers of samples 14+15, in the higher percentage of their time spent

standing near the brood, compared with low activity group VI workers. If "standing around" is a "job", then differences in jobs occur within melanic group VI in this respect also.

The repeated formation under all circumstances of a group of workers standing near the brood suggests that this group has a real sociological significance and does not merely represent workers with nothing else to do, or workers resting etc...

3.—*Worker locomotor activity*.—The locomotor activity of the workers of melanic group VI is considered under three headings: i.—The average length of each trip.—ii.—The total distance covered by the workers of each melanic group divided by the total number of workers in that group (i. e. the length per unit worker of all trips).—iii.—The number of trips. (Table VI and data D.)

(i) There is no variation in the average length of trips by workers of melanic group VI with either time (larval increase in bulk), different group compositions, or with workers from different activity samples. It then seems probable that workers of group VI segregated in activity samples 10+11, were there because of differential sensitivity to stimuli or differences of behaviour (e. g. a tendency to stand near the brood), and not because of significantly higher locomotor activity.

(ii) This also shows no significant variation with any of the factors mentioned in (i) above, and the same conclusions can be drawn.

(iii) This analysis must be considered with caution because the number of trips is small. Analysis, without adjustment for worker number differences, shows surprisingly that there are no significant differences, despite the higher numbers of workers of melanic group VI in nests 1+2. Failure, as in (i) and (ii) [above], of the analysis of the adjusted worker number values to reveal any difference between workers of the two activity levels sampled, leads again to the conclusion stated in (i) above. Differences in the locomotor activity of group VI workers are detectable at the three censuses. These workers show an "initial" level of activity. (The colony fragments were allowed to establish themselves in the nests for twenty-four hours before measurements began.) This "initial" activity level diminishes rapidly in nests 3 to 8, but in nests 1+2 remains at about the same level throughout the experiment. It may be suggested that this "initial" activity is produced by the interaction of larval groups of constant size on workers of melanic group VI (characteristically of low locomotor activity), which have been isolated for several weeks from workers of other melanic groups. Where reintroduction of workers of other melanic groups occurs, the "initial" activity of group VI workers is rapidly lost. It is difficult to visualise worker competition for locomotor activity in a relatively large nest, such as was used in these experiments. Teleologically, therefore, it appears that workers of melanic group VI "prefer" to stay on the brood mass.



*Melanic group IV.*

Data E shows the adjusted number of workers of group IV on the brood mass. Comparison of the unadjusted and adjusted values, shows that while these workers are more often on the brood mass when two are present, the increase is not proportional, and worker number adjustment reduces the value significantly when two workers are present. Therefore, when the number of workers of melanic group IV is increased, there is a change in the proportion of "jobs" carried out.

No differences are detectable in the number of workers of group IV standing near the brood (when the numbers are adjusted).

No differences are detectable in the number of workers of group IV which show locomotor activity (when the numbers are adjusted). But the unadjusted values show that two workers (nests 3+4) make more trips than one (nests 7+8). The total distance covered by these workers is higher in nests 3+4 (data F). Similarly, the average length of trips by these workers is higher in nests 3+4 (data G).

*Melanic group II.*

The only significant difference found in this analysis is that two workers of group II make twice as many trips as one. Therefore, in worker groups of these sizes and numerical relationships, the locomotor activity of individual workers of group II is independent of each other.

**Table VI and associated data.**—Statistical differences attributable to the three census times are of obscure significance. Accordingly, for ease of assimilation, these tables and data show only the average or total values for the three census times.

TABLE VI. — AVERAGE NUMBER OF TRIPS BY WORKERS OF MELANIC GROUP VI DIS-  
REGARDING INITIAL ACTIVITY SAMPLES AND CONSIDERING ONLY THE CENSUSES.

	NESTS.			
	1 + 2	3 + 4	5 + 6	7 + 8
Census 1.	6.6	12.0	20.0	5.0
Census 2.	4.6	1.0	7.0	4.0
Census 3.	7.8	5.0	1.0	2.0

DATA A.—Averaged number of workers of melanic group VI, on the brood mass, unadjusted to worker number. In nests 1 to 8, the relevant numbers of workers were respectively 66.3, 61.6, 52.3, 47.6, 50.3, 46.3, 51.0, 51.0.

DATA B.—Averaged number of workers of melanic group VI, on the brood mass, adjusted to worker number. In nests 1 to 8, the relevant numbers of workers were respectively 46.3, 41.0, 52.3, 47.6, 50.3, 46.3, 51.0, 51.0.

DATA C.—Total number of workers of melanic group VI standing near the brood. Adjusted to worker number. In nests 1 to 8, the relevant numbers of workers were respectively 32, 46, 14, 20, 18, 26, 17, 26.

DATA D.—Total number of trips by workers of melanic group VI. Adjusted for worker number. In nests 1 to 8, the relevant numbers of trips by workers were respectively, 10.4, 9.0, 9.0, 11.0, 17.0, 10.0, 1.0.

DATA E.—Total number of workers of melanic group VI on brood mass. Adjusted for worker number. In nests 3, 4, 7 and 8, there were respectively 24, 29, 40 and 34 workers.

DATA F.—Total distance covered by workers of melanic group IV, divided by the total number of workers. In nests 3, 4, 7 and 8, the distance covered was respectively, 15.8, 9.5, 3.0 and 3.0 units.

DATA G.—Average length of trips by workers of melanic group IV. In nests 3, 4, 7 and 8, the length was respectively, 2.0, 2.9, 1.5 and 1.5 units.

### c) DIFFERENCES BETWEEN MELANIC GROUPS II, IV AND VI

Tables VII.A & B show in tabular form the results of this section of the analysis.

1.—The time spent by workers of the three melanic groups II, IV and VI on the three "jobs" described.—These are shown in table VII.A. It is apparent that while groups IV and VI are comparatively similar (though the differences between these two groups are statistically quite definite), group II shows very different behaviour. This result confirms the differences between workers used in the original segregation.

2.—Effects of group interaction.—The effects on the behaviour of workers of melanic group VI of the presence or absence of workers of other melanic groups, is shown in table VII.B. The overall change in the distribution of jobs is apparent. This may reflect equally the increased numbers of workers of group VI in some cultures as well as the presence of workers of other melanic groups in the other cultures.

Comparable numerical effects in groups II and IV have been demonstrated previously (p. 111).

TABLE VII.A. — % TIME SPENT BY WORKERS IN EACH OF THREE POSSIBLE JOBS.

		"JOB".		
		<i>On Brood.</i>	<i>Near Brood.</i>	<i>Away From Brood.</i>
Worker	II.	8.9	26.3	64.8
Melanic	IV.	73.9	17.4	8.7
Group	VI.	79.2	16.7	4.1

TABLE VII.B. — % TIME SPENT ON "JOBS" BY WORKERS OF MELANIC GROUP VI, IN THE PRESENCE AND ABSENCE OF WORKERS OF OTHER MELANIC GROUPS.

		"JOB".		
		<i>On Brood.</i>	<i>Near Brood.</i>	<i>Away From Brood.</i>
No other melanic groups present		74.1	22.0	3.9
Other melanic groups present		84.4	10.8	4.8

*C. — Brood rearing.*

Larval growth during experiment 4 (described above) was measured in two ways: a. By the increase in weight of each brood mass at each census.— b. By the areal increase of each individual larva at each census as measured by projection of the lateral view.

The use of weight alone as a measure of brood rearing efficiency is here ineffective, since the weight of the larval group gives no indication of the distribution of larval weight gains among the individual larvae. The technique of areal projection of the individual larvae presents difficulties inasmuch as the relationship between area and weight is non-linear. However, a precise relationship can be established and relied upon within the limits of larval turgidity. In view of the close correlation between the measurements of the summed areal increases and the weight gains, only the areal increases are here described.

All larval groups contained, initially, ten larvae, the frequency distribution of larval areas for each group being the same in all eight nests. Four larvae were lost or died during the experiment. Direct statistical analysis of the data would therefore be unreliable. Arrangement of the incremental data for each census in a series of size arrays facilitates estimation of which particular larva has died since the previous census. Some



larvae show negative areal increases, which are statistically intractable. Twenty units have therefore been added to all individual areal increase values to invalidate any negative signs.

Possible errors from these sources have been further reduced by the subdivision of the original array of larval sizes in each group into three sections. i.—Two large larvae.—ii.—Four medium sized larvae.—iii.—Four small larvae.

The incremental data for the larvae within each of these sub-groups has been averaged and is used in the following analysis. Censuses were taken every three days from the start of the experiment. The larval groups were randomised (by tables of random numbers) after the second census and redistributed, after measurement, to the nests. The larval groups were rerandomised after the third census.

This experimental design was defective in that it was not possible to use a Latin square and analyse the effects of both larval groups and worker nests. The use of a Latin square with eight larval censuses is not feasible within the time taken for some of the larvae to reach prepupation, if ethological observations are to be made on the undisturbed colony.

Analysis of the incremental areal data by the partitioning of variance is shown in table VIII, in which the four censuses, three larval sizes, and eight worker nest compositions are all utilised. All the main comparisons are statistically significant, or on the verge of significance, as are all first degree interactions. The situation is therefore complicated, the occurrence of significant interaction having biased the probability of significance of the original comparisons. Re-estimation of their significance is necessary, using weighted measurements. The biological implications (differential treatment of larvae by workers) of the interactions are, however, of fundamental importance, and in this respect re-estimation is unnecessary.

TABLE VIII. — ANALYSIS OF VARIANCE OF AREAL GAINS OF LARVAE USING THE F TEST (SNEDECOR, 1946).

SOURCE.	PROBABILITY OF CHANCE OCCURRENCE.	
	(%)	
Worker groups.	< 10 %	> 5 %
Censuses.	< .1 %	
Larval sizes.	< .1 %	
Groups x censuses.	< 5 %	> 1 %
Groups x sizes.	< 5 %	> 1 %
Censuses x sizes.	< 5 %	> 1 %

The second degree interaction is used as error variance.

Examination of these results shows: i.—There is evidence of consistently "good" and consistently "bad" worker nests as measured by brood rearing success.—ii.—Differing areal increases are achieved by larvae of varying initial size. Large larvae show greater areal gains than medium sized larvae, which, in turn, gain more than small larvae.—iii.—The total areal

gains by larvae at the four censuses are significantly different and can be arranged as follows:

Census number.	4	1	2	3
Total areal increase.	946	662	650	538

The larvae are dehydrated when removed from hibernation for the

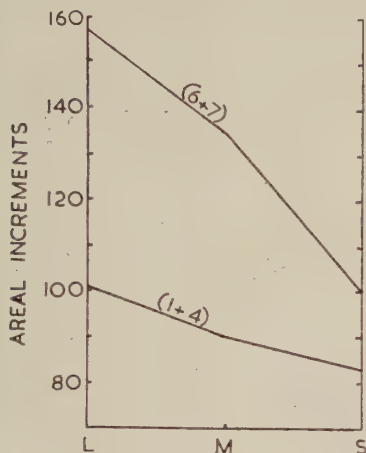


FIG. 3.

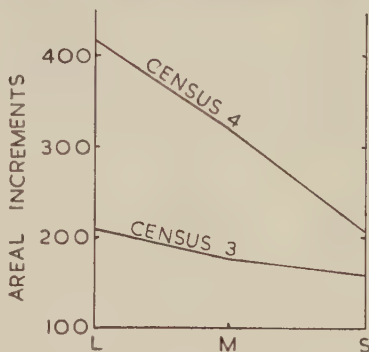


FIG. 4.

FIG. 3, 4 and 5, show diagrammatically the results of larval growth in experiment 4. Areal increments are given in arbitrary units.

3: Variation in areal growth increments of larvae between « good » worker nests (6 + 7) and « bad » worker nests (1 + 4) plotted against larval size.

4: Variation in areal growth increments of larvae between « good » censuses and « bad » censuses plotted against larval size.

5: Variation in areal growth increments of larvae between « good » worker nests (6 + 7) and « bad » worker nests (1 + 4) plotted against « good » censuses and « bad » censuses.

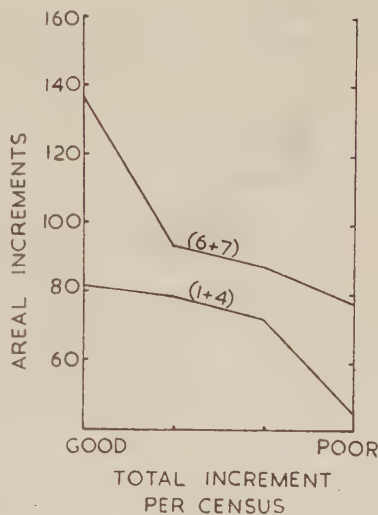


FIG. 5.

experiment, and rehydration is partly measured during the first three days (i.e. during the first census). This causes large areal increases. Growth during the second and third censuses is generally slow since, by chance, larval groups are passed from « good » worker nests to « bad » worker nests and vice versa. During the fourth census, the larval groups show rapid growth and development, particularly in « good » worker nests. The detailed causes of these variations are unknown.—iv.—Interaction between larval size and worker nests is shown graphically in figure 3. Larger differential increases are shown by large larvae in « good »

nesses as compared with "bad" nests, when an overall comparison is made with the corresponding increases for medium sized larvae. Comparison of medium sized and small larvae shows similar results.—v.—Interaction between larval size and census variation is shown graphically in figure 4. When the total areal increase at a census is large, large larvae show relatively higher areal increases compared with large larvae at a census

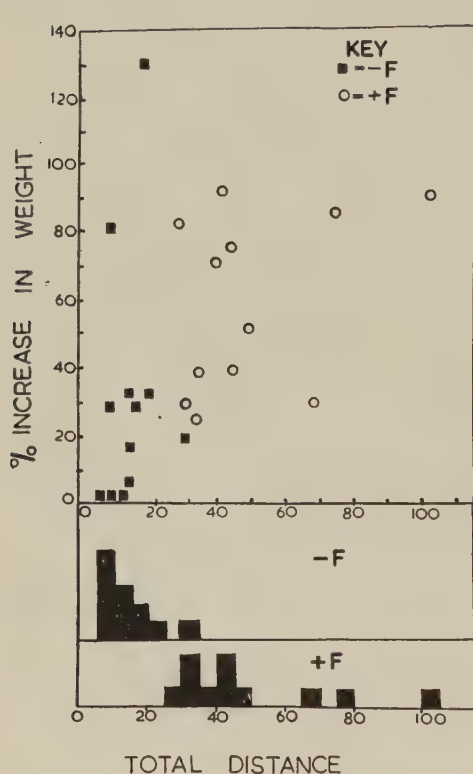


FIG. 6. — Shows the relationship of presence (+) or absence (—) of foragers (F) to percentage increase in larval weight at each census of each brood mass. Values are also shown as histograms.

where the total areal increase is small, comparison throughout being made with the corresponding results for medium sized larvae. These in turn show similar effects relative to small larvae.—vi.—Interaction between censuses and worker nests is shown in figure 5. Where the total areal gain at a census is high, "good" worker nests show large gains compared with "bad" worker nests, comparison being made throughout with similar groups at censuses where the overall areal increase was low.

It is probable from these results, that had the entire experiment been replicated, the error due to variance within groups would have shown that the second degree interaction was also significant. Such a result would imply that in the feeding

The relationship of worker activity and larval growth remains to be



considered. Comparison (figure 6) shows that there is some relationship between the presence of foragers and good larval growth. But the increase in larval growth during any one census may reflect treatment during a previous census in a different worker nest. The necessity for time sequence analysis is apparent, but replication on a larger scale would be essential to such an analysis, since more frequent censuses are impracticable owing to the disturbing effect of these censuses on the workers. There is no direct correlation between worker activity and larval growth at any one census as measured by these methods.

The amount to locomotor activity observed in cultures containing workers of melanic group II greatly exceeds that which might be supposed necessary for normal larval growth as observed in these groups.

#### *D. — Nest building by workers.*

The nest building capacities of the worker melanic groups were investigated in an experiment (5) comprising eight nests. The nests used were first designed by BRIAN (unpublished) and consist of two sheets of glass separated by glass tubing waxed in position round the edge. The dislike of workers for waxed surfaces and bright light can be used to "force" them into a shaded central portion of the nest completely filled with damp artificial soil, composed of kriliun, kaolin, sand and water. When mixed in the correct proportions, these give a moist, friable, easily worked medium for nest construction.

Six workers were used in each nest, two nests containing workers of melanic group III; two, workers of melanic group IV; two, workers of melanic group V; and two, workers of group VI. The results of the experiment are tabulated as observations after four, twelve, twenty-four and forty-eight hours (table IX).

Different melanic groups have different nest constructional capacities. Workers of melanic group III constructed chambers in the open by building walls without excavation of chambers. Workers of melanic group VI showed characteristic aimless soil disturbance and built few chambers. Workers of groups IV and V showed a wide capacity for construction of all kinds of earthworks, chambers, tunnels, etc. There appeared to be excessive nest construction by these workers, far beyond their requirements. Individual workers of these groups would spend hours excavating chambers in the soil, although several chambers were already in existence. In experiment 4 workers of these groups showed most cotton-wool pulling, etc., and this probably represents the same form of behaviour.

TABLE IX. — NEST CONSTRUCTION.

		MELANIC GROUP.							
		III		IV		V		VI	
		Nest.		Nest.		Nest.		Nest.	
		1	2	3	4	5	6	7	8
TIME OF OBSERVATION IN HOURS.	4	w	—	1-C t	—	—	—	—	—
	12	W	W	1-C MT	1-C T	1-C	2-C sd	SD	2-C sd
	24	W	1-C MTw	4-C MTW	3-C MTw	1-C Mw	2-C Msd	SD	2-C MSD
	48	MtW	1-C MTW	6-C MTW	5-C MTW	1-C MW	2-C MSD	SD	2-C MSD
VOLUME.		25 %	30 %	60 %	50 %	20 %	25 %	0 %	20 %

KEY TO TABLE IX.

C = CHAMBERS in the soil (1-C = one chamber; 2-C = two chambers, etc.).

M = MASONRY or individual sand grains pressed into position on the walls of the chambers giving a smooth appearance.

SD = SOIL DISTURBANCE. Scattering aimlessly the soil from the central mass and pushing aimlessly through it (SD = Major disturbance; sd = Minor disturbance).

T = TUNNELS in the soil (T = Major tunnelling; t = Minor tunnelling).

W = WALLS built in open spaces, usually round brood; (W = Major walls; w = Minor walls).

VOLUME of nest filled by earthworks is also shown, e.g. 50 % where volume occupied equalled half the total.

*E. — Worker sizes.*

All workers surviving the period of hibernation and subsequent experiments were measured. High mortality and low initial numbers in

worker melanic groups I, II and III, reduced the significance of measurements in these groups. Information derived from the analysis of melanic groups IV, V and VI only, is described here.

Many varied measurements have been used in the study of polymorphism in ants. The six measurements made on the head and thorax of the *M. scabrinodis* workers may be expected to reveal

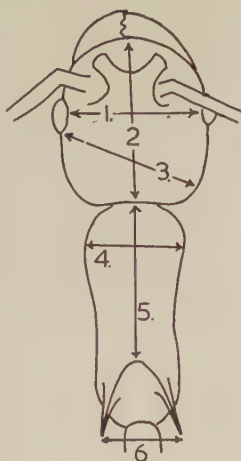


FIG. 7. — Shows six measurements made on the head and thorax of workers of *Myrmica scabrinodis*.

any allometry in these regions (WILSON, 1954). The measurements (figure 7) are: 1. head width (between the eyes). —2. head length,—3. head angulation,—4. maximal thoracic width,—5. thoracic length,—6. distance between tips of the epinotal spines.

Five of these measurements showed simple arithmetic linearity and correlation, but the sixth (epinotal spine width), showed certain irregularities and has, for present purposes, been disregarded. Figure 8 shows the summed values of measurements 1-5 for each worker, plotted against head

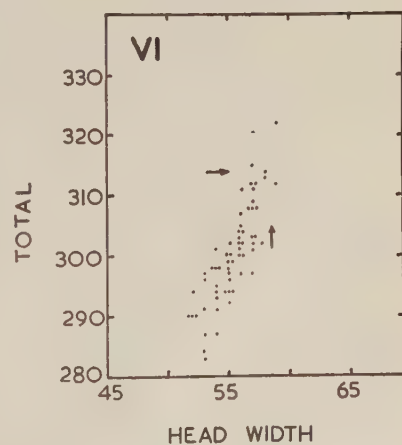
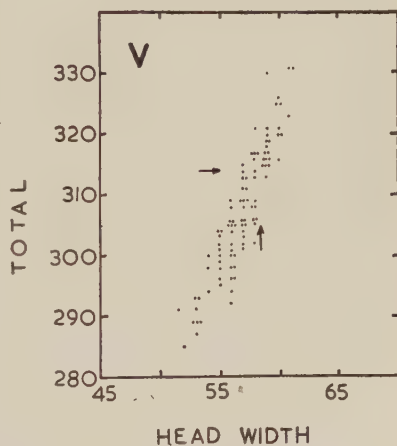
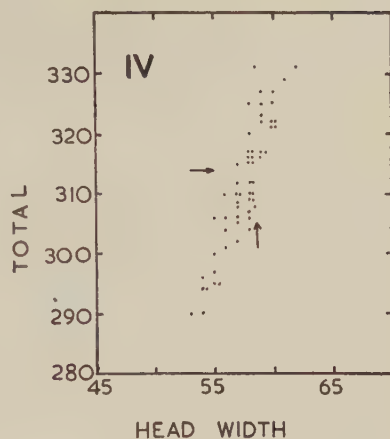


FIG. 8. — Shows the relationship between head width and the sum of the five measurements utilised in this analysis.

1 unit = 0.0154 mm.

The three melanic groups IV, V and VI are considered separately. Arrows delineate that zone which includes 95% of the individuals of melanic group VI. It is apparent from the corresponding arrows on the other diagrams that melanic groups IV and V include many larger individuals.



width. It is apparent that head width provides a reliable estimate of total size, as measured by the five summed values (1-5). No allometry has been detected between these measurements in any of the melanic groups IV, V or VI.

EXAMINATION OF THESE RESULTS SHOWS: a.—There is detectable intranidal variation in worker size.—b.—In the five cases here examined there is no detectable allometry.—c.—There are differences between the frequency distributions of worker size in melanic groups IV, V and VI. Workers of melanic group VI are of smaller average size than those of melanic groups IV or V, which are of similar size ranges.

It is known from observation that workers of melanic group VI are derived from non-dormant larvae of approximately four months previously (mid-summer, 1953). It is also known that workers of group V are derived from the dormant larvae produced during the previous year (1952) and which pupated approximately six months previously (Spring, 1953). If the size differences between groups V and VI reflect consistent differences in the average size of workers produced from non-dormant and dormant larvae, then: i. Workers of melanic group IV are derived from the dormant larvae of two years previously.—ii. Workers of melanic group III may therefore represent the non-dormant brood of that year.—iii.

The rate of melanisation of workers from these two groups must be different, those from non-dormant (III) larvae melanising faster than those from dormant larvae (IV).—iv. The rate of change of social function (job preference) must be correspondingly different since workers of non-dormant larval origin (III) are, within two years, of higher locomotor activity than those of group IV (produced from dormant larvae of the same year).

The relationship of these size differences to the fifteen activity samples of the initial worker segregation is shown in figure 9. This shows the average, for each activity sample, of the total of the first five measurements (1-5 above) on each worker in that sample. Two hundred and thirteen workers were measured, but samples 1, 2 and 8 contained too few survivors for any reliable estimates of average worker size, and this is indicated on the graph. The low average worker size in samples 14 and 15 reflects the low locomotor activity of the small workers of melanic group VI. Seasonal cycles of 'average worker size may be expected among those workers of low activity groups if there are consistent size differences among workers produced from dormant and non-dormant larvae. The uniform distribution throughout activity samples 3 to 15 of the thirty largest

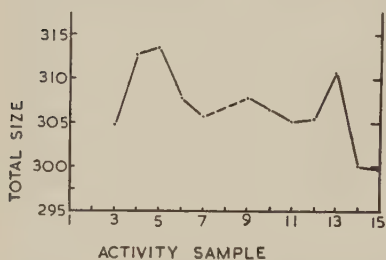


FIG. 9. — The variation of worker size as measured by the total value of the five measurements made, is shown as the averaged sample value plotted against worker activity, as judged from the fifteen activity samples.

workers of melanic group V was equally striking, and gave the appearance, in samples 14 and 15, that larvae were reared by numerous small, pale workers, among which were a few darker workers of much larger size.

#### F. — Discussion of section 3.A=E.

Experiments have shown that the bases of segregation (section 3.A) were justified. Division of labour has been correlated with age and physiology (melanisation) (sections 3.B, D). Older workers have a higher foraging potential than younger workers which tend to stay on or near the brood. These observations are in agreement with those of ERHARDT (1931) on *Myrmica rubra*.

Variation in worker activity and behaviour within certain melanic groups has also been noted in experiment 4. Two possible explanations of this are discussed below. 1. Activity and behaviour of workers of one melanic group may vary with the number of workers of that melanic group present in one colony fragment.—2. Worker job may be altered by the qualitative composition of the colony fragment through worker competition or other means.

Such effects as the change in locomotor activity by workers of group VI (p. 109) may be interpreted on the basis of either explanation, as may the ethological changes shown by these workers (pp. 109 et 110). Differences in the behaviour of workers of melanic group IV are difficult to explain completely except in terms of variation in worker numbers (p. 111). It is also apparent that locomotor activity by workers of group II varies in direct proportion to the numbers of that group present. It appears that workers of group II will always show locomotor activity irrespective of the needs of the colony. Further, workers of group VI always show a tendency to get on top of the brood mass, again, apparently irrespective of the numbers already there. In the absence of workers of groups II and IV, however, workers of group VI can assume all three locational jobs concerned, irrespective of their relative efficiency in these jobs.

Such ethal plasticity may only be interpreted in terms of a system of dynamic worker-job-preference. Any such system of dynamic worker-job-preference is related, in some cases, to factors such as the total size of the brood mass, which may be limiting. This will inevitably result in the incidence of quantitative effects. Therefore the two possible causes of variation noted above are not mutually exclusive and may well be interdependent.

Job preferences can be expressed as the percentage time spent in any "occupation", since all workers appear capable of participating in any "job" at any time. Workers of melanic groups I, II and III, appear to have a preference for locomotor activity. These workers may be considered as "foragers" since high locomotor activity outside the brood chamber automatically increases the chances of contact with potential environ-

mental food (p. 102). Workers of groups IV and V (i.e. those shown to stand around the brood mass, and also to have a low degree of locomotor activity) show a preference for nest construction (experiment 5, section 3.D above). It should be noted that in experiment 4 there was no "outlet" for the energy of workers preferring to construct nests (p. 117). Workers standing around the brood mass in laboratory nests may well represent an unemployed group which would prefer to build nests, and may be characteristic only of laboratory conditions. These groups may be designated "domestics".

Finally workers of melanic group VI have been demonstrated to have a preference for standing on the larval brood mass (experiment 4), and may be considered as "nurses". These conclusions are incorporated in table X.

It should be noted that workers of melanic group IV show, in excessive

TABLE X. — WORKER MELANIC GROUPS AS FOUND IN A COLONY IN THE AUTUMN OF YEAR X.

	MELANIC GROUPS VI and V.	MELANIC GROUPS IV and III.	MELANIC GROUPS II and I.
Time of pupation on the basis of constant melanisation rates.	Workers produced during current season. Year (x).	Workers produced during previous season. Year (x-1).	Workers possibly produced two seasons previously. Year (x-2).
Preferential job.	On brood mass (Nurses.)	Nest construction. (Domestics.)	Locomotor activity. (Foragers.)
Groups III is anomalous, since in the initial separation it shows the characteristics of foragers. This is discussed below (p. 124), as is the problem of the time of origin of workers of groups I and II.			

nest construction, the same occupational "exuberance" shown by workers of group II in excessive foraging, and workers of group VI in standing on top of the brood mass. It appears that the activity and behaviour of individuals of these worker groups when engaged in their preferential occupation is a factor of the total number present. In the absence of workers of certain other melanic groups ethological plasticity is apparent, but the differential behaviour shown may not then be dependent on worker number.

Finally, it may be suggested that the location in the laboratory of a proportion of workers of melanic group IV round the brood mass, indicates that this middle-aged group, potentially the most plastic ethological group in the nest, represents the mobile worker reserve of the colony which can



be changed from one job to another according to the needs of the colony. This provides some explanation of observations such as those of EIDMANN (1927) on foraging recruitment in *M. laevinodis*. The presence in the colony of a small number of workers of permanent high locomotor activity which, on the detection of suitable food, stimulated large numbers of unemployed workers in the nest and enabled these latter to find their way to the food by a scent trail (CARTHY, 1950), would provide a very efficient mechanism of forager recruitment without excessive and wasteful energy expenditure.

Theoretical worker-job-preferences have been utilised (RIBBANDS, 1953), to explain the time sequence of worker duty in *Apis* colonies (ROSCH 1925; LINDAUER, 1952). Similar job-sequence conditions have been reported in *Polistes* (STEINER, 1932), and in various ants by FOREL (1874), BUCKINGHAM (1910) and HEYDE (1924). The normal job sequence in these ants follows that described by EHRHARDT (1931), in *Myrmica rubra* and reinvestigated by the present author in *Myrmica scabrinodis* (part I, above) and in *Myrmica rubra* (part II of this report).

Such widespread occurrence of this social mechanism justifies usage of the word polyethism to describe, in species which may be monomorphic, the condition of worker-job-preference alteration with age, accompanied by the retention of a high degree of ethological plasticity.

The association of such systems of worker polyethism with monomorphism has been indicated by RIBBANDS (1953) and SCHNEIRLA (1953, in ROEDER, 1953) among others. While the investigations described in section 3.E above show that *M. scabrinodis* is a characteristically monomorphic species, there are size differences between the melanic groups concerned. Noteworthy is the association of larger individuals with nest construction. The occurrence, in polymorphic species, of phragmotic majors is well known (*Camponotus* [*Colobopsis*] WHEELER, 1910; FOREL, 1921; and CREIGHTON, 1953), as is the association of large workers with nest construction (*Oecophylla*, DOFLEIN, 1905).

The time of origin of melanic groups I and II is doubtful. BRIAN (1951 *b*) considers maximal imaginal worker life to be two years in *M. laevinodis*. The problem of melanisational causality then arises. There are two possibilities. Does increased locomotor activity cause increased melanisation, or does melanic change accompany ethological change depending solely on worker age? Considering the latter possibility if constant rates of melanisation of the *M. scabrinodis* workers are assumed (p. 104), the time of origin of workers of melanic groups I and II may be three years previous to the time of experimentation (table X). But if the evidence of the size analysis of workers (section 3.E, p. 120 above) is accepted as showing that melanic group IV represents workers produced from the dormant larvae of the preceding year, then group III must represent workers derived from non-dormant larvae. Further, acceptance of this hypothesis implies that, during a period of two years, these two worker groups have reversed their original melanic differences as

determined by the time of pupation, and that small workers derived from non-dormant larvae have a higher rate of cuticular melanisation compared with workers derived from dormant larvae. In addition, the rate of change of functional preference would have to be faster in non-dormant workers (group III). Such effects would be consistent with a continuation into imaginal life of differing rates of tissue differentiation established in the larva, since ethological change in the worker may well be connected with temporal change in the nervous system.

If constant melanisation rates do occur, then workers of groups I and II may be three years old. But if individual activity is responsible, groups I and II may represent a few individual workers of any age group which, for unknown reasons, show inherent high locomotor activity, and so have become strongly melanised foragers. In this connection it is of interest to note that melanisation may be affected by cestode parasitisation (Muir, 1954). Again, however, high locomotor activity accompanied by strong melanisation may expose certain individuals to a greater risk of infection. It remains possible that melanisation reflects an ineffective disposal of residual metabolic waste, and may therefore result from a drain on anabolised material caused by such factors as continued oviposition, parasitisation or high locomotor activity. Since worker oviposition utilises fat body, it is conceivable that there exists in the imago physiological competition between organ systems, comparable to that which may be supposed to occur in the larva (i.e. between the imaginal rudiments and the larval fat body), where it is partially controlled by the retrocerebral endocrine system. Also, it seems probable that the imaginal cuticle acts as a dumping ground for waste material (storage excretion).

Finally, the significance of periodic worker recruitment must be considered. New workers are produced in two brood batches during the summer. The first consists of workers produced from dormant larvae, the second of workers from non-dormant larvae. Observation in other colony fragments of *M. scabrinodis* shows that both groups of recently emerged callow workers (three weeks old) show a strong preference for brood rearing. (The first fourteen days of imaginal life are also spent on the brood mass but workers may not contribute actively to brood rearing during this period.) The possibility of seasonal cycles of size variation among nurses has been indicated. Further, the sudden influx of a group of workers into an occupation representing one end of a dynamic preferential system cannot fail to influence the numbers of workers engaged on the other occupations if some social mechanism like worker competition for job preferences is present, i.e. an influx of nurses will cause a corresponding though smaller increase in the number of domestics, and this in turn may affect the numbers of foragers. Such effects on worker foraging would be independent of the foraging activity of melanic groups at the extreme end of the worker ethological scale (i.e. the confirmed and preferential foragers), but would increase the percentage time spent in foraging by plastic, middle-aged workers.

Thus social periodicity might be initiated by the temporal separation of brood masses. The causes of periodicity in the production of larvae will be considered elsewhere. Cycles of queen oviposition, larval growth and foraging activity in sub-tropical conditions have been extensively described in *Eciton* by SCHNEIRLA (1953, and previous papers). The hypothesis outlined above supplies an interesting comparison with the sub-tropical work of SCHNEIRLA, and shows how adverse microthermal conditions, necessitating the overwintering of larvae, may in this case initiate social periodicity.

Comparison of the activity measurements with the results of the brood rearing analyses are disappointing. It appears that much of the locomotor activity shown by the workers is excessive, compared with the growth shown by the appropriate larval groups. One experimental difficulty arises from the provision in all these nests of an abundance of environmental food, easily accessible even to workers of low locomotor activity. Results described elsewhere by the present author and BRIAN (personal communication) show that compared with conditions in the field there is an excessive food flux in these nests as measured by the quantitative development of the larval fat body and the gut. The effects of differential worker activity, probably important in nature, will tend to be obscured in the laboratory. Experiments on these lines of investigation using colonies of *M. rubra microgyna* will be described elsewhere.

While abundant environmental food near the brood chamber has masked the differential effects on larval growth which might be expected in nature from nests containing these proportions of worker types, the importance of worker-laid eggs and worker glandular secretions as larval food must not be overlooked. While larval growth may be augmented by extra-sociological (environmental or allochthonous) food procured in certain cultures by workers of group II, it may be augmented to an equivalent extent by sociological (autochthonous) food (e.g. eggs or glandular secretions) if these are produced by workers of group VI. Such differences in egg production are described in part II, section 4.E of this paper. If such a dual origin of larval food causes differences in larval growth these may be qualitative, not quantitative, and will be affected by changes in the proportions of worker types present. There can be little doubt that the polyethal worker conditions here demonstrated have critical effects on larval growth and development in nature.

### *Summary of part I.*

Variation in worker locomotor activity and worker behaviour in *Myrmica scabrinodis* has been experimentally investigated.

1. Three worker jobs are recognised. Workers doing these jobs have been designated nurses, domestics, and foragers. Differences in locomotor



activity, behaviour, brood rearing, size, and nest-building capacity have been recorded.

2. Worker-job-preference (worker polyethism) has been demonstrated forming a dynamic system.

3. Worker-job-preference changes with age in the sequence nurse → domestic → forager.

4. Ethologically domestics are most plastic and are preferential nest builders.

5. Cuticular melanisation increases as ethal changes occur.

The significance to be attached to the rate of cuticular melanisation, to size variation and to ethal differences between melanic groups is discussed.

### *Résumé de la première partie.*

Étude expérimentale chez *Myrmica scabrinodis* du comportement et de l'activité locomotrice des ouvrières.

1. On reconnaît trois tâches aux ouvrières, qui sont dénommées sur cette base nourrices, ménagères, fourrageuses.

On les compare au point de vue de leur activité locomotrice, de leur comportement, de l'élevage de la couvée, de leur taille et des moyens de construction de nid.

2. On démontre une liaison préférentielle ouvrière-tâche (polyéthisme) sous forme de système dynamique.

3. La liaison ouvrière-tâche se transforme avec l'âge selon la suite nourrice → ménagère → fourrageuse.

4. Les ménagères s'adaptent mieux aux changements éthologiques et marquent une préférence pour la construction des nids.

5. Le mélanisme de la cuticule s'accroît avec les changements de mœurs.

On discute les valeurs respectives du taux de mélanisme, de la variation de taille et des divergences éthologiques des différents groupes mélaniques.

### *Resumen. — Sección I.*

De forma experimental, se ha investigado la variación en la locomoción y comportamiento de la trabajadora *Myrmica scabrinodis*.

1. Se reconocen tres labores entre las trabajadoras y aquellas que las ejercen se dividen en: domésticas, enfermeras y forajeras. Se anota una diferencia entre su actividad, comportamiento, tamaño, cuidado de su cría y capacidad de anidación.

2. Preferencia de labor (polyetismo) demuestra un sistema dinámico.

3. Esta preferencia cambia con su edad: de enfermera → domestica → forajera.
4. Etologicamente, las domésticas son las más maleables, siendo preferentemente anidadoras.
5. Su melanización cuticular aumenta al ocurrir los cambios etales. Se comenta sobre el significado ateniende a la proporción de melanización cuticular, variación de tamaño y diferencia etal entre los grupos melánicos.

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# OBSERVATIONS ON THE BEHAVIOR OF THE CERAPACHYINE ANTS

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Although the cerapachyine ants range widely through the tropical and subtropical regions of the world and are even abundant in some local areas, they have long remained among the most poorly known of the major ant groups. With the exception of the published observations of W. M. WHEELER and John CLARK on *Phyracaces* (see below), there has been virtually no usable information on cerapachyine behavior available in the literature. During a recent research tour in Melanesia and Australia, the present author had some excellent opportunities to make observations on species of *Cerapachys*, *Phyracaces*, and *Sphinctomyrmex* under field conditions. The new information obtained along with some valuable unpublished notes on *Sphinctomyrmex* supplied the author by W. L. BROWN, is presented in the sections to follow.

## *Cerapachys (C.) flavaclavata* Donisthorpe.

*Cerapachys (C.) flavaclavata* Donisthorpe, 1938, Ann. Mag. Nat. Hist., (11)2: 499, worker. Type locality: Sabron, 350 m, Cyclops Mts., Neth. New Guinea (Syntype examined).

This tiny species was collected by the author during May, 1955, in primary rainforest at the Busu River, near Lae, northeastern New Guinea. One colony (my accession no. 985) was discovered while in the act of raiding a colony of a small species of the ant genus *Pheidole*. When first encountered, during late afternoon of a sunny day, the raid was evidently already in full swing, and activity continued for at least another half hour. At maximum activity during this time, the *Cerapachys* workers were running in a loose file on an average of two to three centimeters apart, but toward the end of the observation period the intensity of the raid had declined to the extent that workers were spaced on an average of approximately thirty centimeters apart. The raiding trail ran from a cluster of small rotting twigs and branches in leaf litter, beneath which the *Cerapachys* nest seemed to be located, up over some dead leaves and onto a nearby small dead branch lying on the ground, down the length of this branch for twenty to thirty centimeters, over to another small branch and down its length for another twenty to thirty centimeters, and finally

down onto the ground in the vicinity of the *Pheidole* nest. It was clear that the *Cerapachys* workers had followed the most open, unobstructed ground route between the two nests in conducting the raid. They were moving at a fast, steady pace, never stopping along the way, even when they encountered a sister worker coming from the opposite direction. Approximately one-third of the homeward-bound workers were laden with pupae and mature larvae of *Pheidole*. At the height of the raid, about ten to fifteen *Cerapachys* workers could be seen at any given moment loitering in the vicinity of the *Pheidole* nest entrance; others were turned up inside the *Pheidole* nest when the latter was excavated at the end of the observation period. A number of *Pheidole* minor workers were walking about outside the nest carrying their own brood, a form of escape behavior common in ants being raided by other ant species. No *Pheidole* major workers were in evidence above ground, and there was no sign that members of this caste had offered any resistance to the *Cerapachys* within the interior of their nest.

When the raid had diminished in intensity, the author opened the *Pheidole* nest by digging in from the side. The main part of the colony was found in galleries and chambers about ten centimeters beneath the soil surface. Workers of *Cerapachys* were found only in the upper, more sparsely populated part of the nest, where they were evidently engaged in robbing from smaller, peripheral groups of brood. No attempt was made at this time to locate and excavate the *Cerapachys* nest. Several days later this sector of the forest was revisited, but no further sign of the *Cerapachys* could be found, even when the soil was turned over in the spot where the *Cerapachys* nest had appeared to be located previously.

### *Cerapachys (C.) opaca* Emery.

*Cerapachys opaca* Emery, 1902, Természet. Fü., 25: 153-154, worker.  
Type locality: Sattelberg, northeastern New Guinea.

This black, medium-sized species was collected in the rainforest at the Busu River, northeastern New Guinea. One colony (accession no. 921), comprising a single nest queen and 75 to 100 workers, was found nesting in several poorly defined galleries beneath the bark of the lower surface of a rotting log. Brood was present and consisted of numerous small larvae, all of which were about the same stage of development. Scattered among the brood were mature larvae, worker pupae, and adult workers of the dacetine ant species *Strumigenys loriae* Emery. This prey was fresh and gave evidence of having been secured in a recent raid. Some of the *Strumigenys* pupae had been mangled and partly eaten.

*Phyracaces cohici* Wilson.

*Phyracaces cohici* Wilson, 1957, *Breviora*, no. 74: 1-4, fig., worker, male.  
Type locality: Ciu, New Caledonia.

This recently discovered species was found to be abundant in the sub-tropical evergreen forest that extends south of the Canala River in New Caledonia. The holotype colony (acc. no. 263) was nesting in the soil under a rock in a densely shaded part of the forest. It occupied a single chamber beneath the rock and an adjacent short, vertical gallery. Males present in the nest were very active and attempted to fly when uncovered. Another colony (acc. no. 246) was nesting in open soil in a partial clearing at the side of a native trail. The nest entrance consisted of a single hole, five millimeters in diameter, surrounded by a low, irregular turret of excavated earth. On January 3, 1955, toward the end of the author's stay at Ciu, the nest was opened by digging from the side. Part of the nest structure thus revealed included three or four galleries leading down away from the nest entrance into soil between several buried rocks. Approximately ten centimeters beneath the surface were located two small, adjacent chambers that had been excavated next to the vertical face of one of the rocks. In these were crowded most of the workers and all of the brood. At the time of collection the following population estimate was made: 80-100 workers, 40 worker pupae (in cocoons), 30-40 half-grown to mature larvae, and 30 eggs. No reproductive was found.

On December 31, 1954, the abovementioned colony (no. 246) was found in the act of raiding a nest of a small species of *Pheidole*. The *Phyracaces* workers were running in a nearly straight line over the surface of the ground back and forth to the *Pheidole* nest, which was in the soil beneath a pile of leaf litter approximately seven meters away. They gave the impression of orienting by an odor trail, since as they ran they palpated the ground constantly with rapid movements of their antennae. Few deviated from the main route, and then only for short exploratory trips to the side.

The raid was first noticed at 12:10 p.m., at which time it was mounting in intensity. By 12:50 it had reached maximum intensity. At this point workers were travelling along the trail in both directions and were spaced at intervals averaging roughly eight to ten centimeters. They were moving at a leisurely but steady pace, covering approximately sixty centimeters a minute. About twenty *Phyracaces* workers were milling around the *Pheidole* nest entrance, and ten more around the *Phyracaces* nest entrance. Several *Pheidole* minor workers, laden with brood, were seen wandering over the ground in the vicinity of their own nest. No combat between *Phyracaces* and *Pheidole* workers was observed. Approximately one in every five of the homeward-bound *Phyracaces* was carrying a *Pheidole* larva or pupa in its mandibles.

The raid was continuing in full swing when I left the scene temporarily



at 1:00. At 1:40, when I returned, the raid was found to have ceased. A few *Phyracaces* workers were observed wandering about in the vicinity of both nests, but the transport of *Pheidole* had evidently stopped.

The next day (January 1, 1955) I returned to the same spot in the early morning (8:25 a.m.), before the rays of sun had reached this part of the forest, and while the vicinity of the *Phyracaces* nest was still relatively cool and dark. At this time a raid was already in progress. The *Phyracaces* workers were moving along the same trail used the previous day. Several workers were returning with *Pheidole* larvae. Outgoing workers were rather scarce and could not be traced to within more than three meters of the *Pheidole* nest raided the day before, and no *Phyracaces* were uncovered in the vicinity of this nest. The conclusion was drawn that the activity observed represented the terminal stages of a raid. The *Phyracaces* nest was kept under observation for the remainder of the morning and part of the afternoon, during which time the *Phyracaces* remained within the confines of their nest.

The next day (January 2) I arrived at the nest site at 8:10 a.m., with the hope of remaining there until I could observe the development of a raid. This attempt was rewarded, for activity commenced shortly thereafter. At 8:25 the first worker emerged from the entrance of the nest and began sluggishly wandering around in the immediate vicinity. During the next hour several more workers made their appearance, wandered about for a short while, and reentered the nest. At 9:28 one worker began moving up the thin, dead vine stem that had served as the starting point of the raiding trail on the two previous days. This initial forager ventured only a few centimeters out on the stem, then turned around and came part way back. At 9:30 a second worker started out on this route and soon met the first. Immediately thereafter a party of thirteen additional workers, which had meanwhile emerged from the nest, mounted the vine and moved up it to meet the two original foragers. The entire party now moved further along the vine to a point, fifteen centimeters from the nest entrance, where the original raiding trail continued on to an adjacent vine. Here the party halted, and after a moment of hesitation several of the workers mounted the second vine, continued down its length, and stepped down onto the surface of some adjacent dead leaves that marked an extension of the original raiding trail. These ants moved cautiously, rapidly palpating the ground before them, and gave every impression of following a previously set odor trail.

In the meantime other workers were emerging from the nest and moving onto the raiding trail. A few were wandering in other directions, some as far as thirty centimeters from the nest entrance. By 9:40 there were approximately fifty workers outside the nest, and a majority was moving in a steady stream back and forth on the raiding trail. A few had reached a point sixty centimeters from the nest entrance. There was clearly no individual leadership involved in this movement. Rather, the ants were progressing as a group, with individuals running back and forth for

various distances and frequently halting altogether for short intervals. At the head of the column, first one worker and then another moved into the lead, pressing ahead on its own for a short distance and then turning back to relinquish its lead to the next worker in line.

By 10:00, the workers were showing a marked tendency to disperse from the old raiding trail. There were many brief excursions to the side of the trail, during which a worker would wander off to the side by itself, cautiously exploring the ground with its antennae. Often it would be followed by one or two other workers that picked up and followed its odor trail. In most cases, these little foraging parties turned back after a brief exploration, but many continued on to effect a partial dispersion of the original foraging column. Some of the workers were observed as they made accidental contact with individual foraging workers of *Leptomyrmex pallens* Emery and *Xiphomyrmex tenuicrinis* Emery; in every case the *Phyracaces* showed a strong avoidance reaction.

By 10:25 two workers had reached a point on the old raiding trail approximately two meters from the home nest entrance. At 10:41, more than two hours after the mass foraging had begun, a few workers were seen moving back and forth on the trail at a point three meters from the nest entrance. Behind them the other workers had continued to disperse from the raiding and secondary trails until the entire party was scattered in all directions around the nest area, and a majority of the workers were exploring either on their own or in small parties. Most were still concentrated within two meters distance of the home nest. This pattern of foraging activity continued for the remainder of the morning, beginning to decline about noon. Evidently no nest suitable for raiding was found during this time, for no raid developed during the rest of the day.

One other colony of *Phyracaces cohici* (acc. no. 298) was found while engaged in a raid and is worthy of special mention. The workers were encountered at 2:30 p.m., evidently in the terminal stages of a raid on a nest of *Pheidole xanthocnemis* Emery. Only a few individuals were running along the raiding trail. One was carrying a pupa, another the gaster and pedicel of an adult *Pheidole* major worker.

### *Phyracaces dumbletoni* Wilson.

*Phyracaces dumbletoni* Wilson, 1957, Breviora, no. 74: 5-7, fig., worker, ergatogyne. Type locality: Chapeau Gendarme, New Caledonia.

This large species occurs in both the dry, semideciduous, "valley-pocket" forest of southwestern New Caledonia and the moister broadleaf evergreen forest near Ciu on the east coast. The type colony (accession no. 65) was nesting in several spacious galleries and chambers in the upper layers of a large, moist, fern-covered log. It contained at least 200 workers, a single ergatogyne, over 100 cocoons and larvae of various ages,

and an indeterminate number of eggs. Among the the brood were found the hollowed-out propodeum of a worker of an undescribed species of *Lordomyrma* and a *Lordomyrma* worker prepupa. These insects appeared to be the prey of the *Phyracaces*.

***Phyracaces* sp. near *punctatissima* Clark.**

The raid of a large, light reddish *Phyracaces*, apparently an undescribed species related to *P. punctatissima* Clark, was witnessed by Mr. Athol Douglas and the author near Balladonia, Western Australia, on February 13, 1955. The colony (acc. no. 445) was encountered in arid *Eucalyptus* woodland at 5 p.m., in the late afternoon, when the diurnal ant fauna of the area was still actively foraging. At this time the raid appeared to be in its terminal stages. The raiding file consisted of homeward-bound workers spaced at intervals averaging roughly ten meters. These individuals were travelling rapidly in a straight line toward the home nest. Circumstances were such that it was impossible to tell whether they were following an odor trail or orienting visually. Four of the workers were carrying prey, consisting in each case of the gaster and pedicel of a worker of an unidentified species of the formicine genus *Melophorus*. The raided nest could not be found. The exterior of the *Phyracaces* nest consisted of an unadorned hole in the bare earth, just wide enough to admit a single worker at a time. From the entrance hole several galleries penetrated into the soil to a depth of about fifty centimeters. The entire colony was recovered by digging; it contained a single dealate queen and approximately thirty-five workers.

**OTHER SPECIES OF *PHYRACACES***

The observations on *Phyracaces* recorded above are not the first to have been made on the behavior of this genus. In 1918 W. M. WHEELER described the raid by a colony of *P. ficosus* Wheeler on the nest of a small, undetermined myrmicine. About a dozen of the *Phyracaces* workers were found running in a loose file, several carrying pupae of the raided species. Wheeler found a few other species of *Phyracaces* group-foraging during the daytime, and, although no other raids were seen, he predicted that as a rule "the large-eyed *Phyracaces* forage in troops (or as whole colonies ?) on the surface of the ground, their prey consisting of the brood of other ants." This prediction has been fully verified by later studies.

After WHEELER's initial observations, CLARK (1923, 1924, 1941) added significantly to our knowledge of *Phyracaces* biology. Following extensive experience in the field with many of the Australian species, CLARK stated that the members of the genus are generally robber ants, and in South-western Australia at least show the following additional peculiarities:



Most of the smaller species may be found early in the morning from daybreak to eight or nine o'clock, and in the evening from about five o'clock until dark, when they are out raiding the nests of other ants. The larger species are frequently found raiding nests during the hottest part of the day. The nests are generally indicated merely by a small entrance on the surface of the ground, with no mound or other sign that a nest exists; occasionally they are found under stones or logs; as a rule, the nest extends about one foot below the ground level.

The *Phyracaces* Clark studied preyed on species of *Iridomyrmex* and *Crematogaster*. Workers of some of the species, e.g. *O. simmonsae* Clark, foraged as a group, but others, such as *P. punctatissima* Clark, seemed to forage singly.

CLARK's observations on the raiding behavior of *P. simmonsae* are of sufficient interest to deserve quoting here:

The colony taken at Mundaring was noticed whilst its members were raiding a nest of *Crematogaster rufotestaceus* MAYR, and were traced to their nest, about thirty yards away. The *Phyracaces* were taking both larvae and pupae from the *Crematogaster* nest, and apparently got very little opposition from the ants of the latter nest, who seemed to concentrate their energy to removing the brood. The *Phyracaces* did not move in a body, but worked much as do the species of *Iridomyrmex*, a constant stream of ants coming and going between the two nests with usually a gap of many inches between the workers. The nest of *Ph. simmonsae* was very inconspicuous, being indicated merely by a small hole, less than one quarter of an inch in diameter, on level ground. This nest extended underground for eleven inches, ending in an elongate chamber where the female and her brood were found. A number of *Crematogaster* larvae and pupae were also found in the chamber.

Field notes on *Phyracaces* (*Neophyracaces*) *potteri* Clark supplied CLARK by the collector, Mr. H. POTTER, contain some important details, including the only available description of the early stages of a complete cerapachyine raid. The type *potteri* nest was found in open, cultivated land, and its exterior consisted of a single, inconspicuous hole in the ground. The colony was observed conducting a raid on the afternoon of January 21, 1934. Following is an excerpt of POTTER's notes dealing with this event:

A few workers, each with its abdomen raised upwards, were moving rapidly about. At 3 p.m., with the shade temperature at 90° Fahr., a large number of the ants was seen leaving the nest and travelling to a series of nest holes about twenty-two yards away. The series of nests belong to a small dark coloured ant [*Iridomyrmex viridigaster* Clark]. On reaching these nests the robbers did not hesitate, they went boldly in and apparently got little resistance as they soon emerged again each carrying a larva or pupa of the *Iridomyrmex* with which they returned to their own nest. Little or no order was maintained during the raids, each ant seemed to work independently, but a constant stream kept on coming with nothing and returning with larva or pupa. Later, at 4 p. m. there was no sign of the robbers near the nest which they had been robbing; apparently the raid had ceased.

*Sphinctomyrmex steinheili* Forel

*Sphinctomyrmex (Eusphinctus) steinheili* Forel, 1900, Ann. Soc. Ent. Belg., 44: 72, worker (ergatogyne?). Type locality: Mackay, Queensland.

The following observations are based on unpublished field notes by Dr. W. L. BROWN, who has generously supplied this information for inclusion in the present paper. BROWN found *S. steinheili* relatively common in both wet and dry sclerophyll forest and in open bracken woodland in localities that he visited in the Melbourne area, Western District of Victoria, and southeastern Queensland. Colonies were nesting under rocks and in rotting wood, and the adults and brood of individual colonies were usually all massed together in a single chamber. In at least one case there was evidence that the ants had excavated part of the nest themselves. Each colony contained multiple ergatogynes, and the brood of a given colony was always developmentally synchronized.

At Dandenong Creek, Vermont, Victoria, Brown witnessed the raid of a *steinheili* colony against the colony of a species of the formicine genus *Stigmacros* (probably *S. impressa* Forel). When first encountered, in the mid-afternoon, the raid was already past its peak. The *Sphinctomyrmex* were running at intervals along the bottom of cracks in dry clay soil, and a minority of the homeward-bound individuals were carrying *Stigmacros* pupae. The raided *Stigmacros* nest was situated in the soil at the base of a tree. A number of *Stigmacros* workers were seen running over the ground in the vicinity, many carrying larvae and pupae in their mandibles.

*Sphinctomyrmex caledonicus* Wilson.

*Sphinctomyrmex caledonicus* Wilson, 1957, Breviora, no. 74: 8-9, worker, ergatogyne. Type locality: Ciu, New Caledonia.

This species was found only in a small, isolated patch of disturbed woodland at Ciu. It was never encountered in the nearby Canala River forest, where *Phyracaces cohici* abounds, despite an intensive search for it there. The several colonies collected were all quite large and contained multiple ergatogynes, as well as large quantities of developmentally synchronized brood. Portions of two colonies were airmailed to Dr. W. L. BROWN and Mr. R. B. WILLEY, at Harvard University in the United States, in the hope that these investigators would be able to carry on an ethological study of the species under more leisurely laboratory conditions. Unfortunately only a few workers and ergatogynes survived the two-weeks trip (in the case of the principal observation colony, 24 workers and 4 ergatogynes), and these lived in the laboratory for only a little more than

a month thereafter. Nevertheless, during this time BROWN and WILLEY were able to make some suggestive observations on the behavior of this species, which with their permission I have undertaken to summarize below.

The *Sphinctomyrmex* were offered a variety of small insects, including adult workers and brood of the ants *Myrmica rubra* L., *Lasius alienus* (Foerster), and *Acanthomyops claviger* (Roger). Only the ants were accepted as prey. The *Sphinctomyrmex* workers did little foraging within the confines of the artificial nest, but when by chance they encountered other ants they attacked these insects immediately. The attack movement included lunging, seizing with the mandibles, and stinging. The *Lasius* were often able to counter effectively by spraying the *Sphinctomyrmex* with formic acid, which substance sometimes temporarily incapacitated the cerapachyines but rarely seemed to injure them permanently. After such engagements, the *Sphinctomyrmex* workers were seen to intensify their usually incessant grooming activities, evidently in an attempt to remove the acid. Captured worker ants were carried into the brood chambers of the artificial nests, their gasters or heads chewed off, and their soft internal parts eaten by the *Sphinctomyrmex*. Larvae of other species were accepted by the *Sphinctomyrmex*, placed among the *Sphinctomyrmex* brood, and eventually eaten.

The ergatogynes displayed a behavioral character worthy of separate mention. These individuals never left the brood chambers to forage on their own, but remained closely associated with the brood, wrapping their long, slender bodies around small piles of larvae and eggs. This unusual protective posture was also frequently assumed by inactive workers.

## DISCUSSION

It is most significant that all of the cerapachyine prey records accumulated to the present time involve other ants. Moreover, it is clear that some of the species, e.g. *Cerapachys opaca* and *Phyracaces cohici*, capture not only larvae and pupae but adult workers as well. Whether this myrmecophagous habit is universal among the cerapachyines can be decided with assurance only when information is made available on the other principal cerapachyine stocks, including the aberrant genera *Acanthosticus* and *Lioponera*.

*Phyracaces*, the genus about which we know the most, shows considerable latitude in prey choice, various species attacking assorted members of the subfamilies Myrmicinae, Dolichoderinae, and Formicinae. Due to the scattered nature of the observations, however, little information is available on the prey-specificity of individual species of *Phyracaces*. It may be significant that both prey records of *P. cohici* involve species of *Pheidole*, but it still remains to be seen whether this myrmicine genus is the exclusive or even the preferred prey. A fascinating possibility to be



examined is that the two New Caledonian species of *Phyracaces* have mutually exclusive prey choices, the smaller *P. cohici* specializing on species of *Pheidole* and the larger *P. dumbletoni* on the correspondingly larger species of *Lordomyrma*.

The raiding expeditions of *Cerapachys* and *Phyracaces* described herein contain some features worthy of special discussion. The workers of individual colonies were clearly raiding synchronously and as a group (group-predation), a somewhat rare behavior pattern which I have elsewhere (WILSON, 1957) suggested as one of the basic criteria of the "army-ant" adaptive type. The extent to which this behavior form is associated with frequent emigration (nomadism) is not known, but there is an excellent chance that group-predation and nomadism are generally associated where either occurs in the Ponerinae and Cerapachyinae. An extended study of the day-by-day activity of some cerapachyine species, to determine whether it is nomadic in habit in addition to being group-predatory, is clearly needed. As pointed out in the abovementioned paper, the primary adaptive significance of group-predation (and possibly the whole of army-ant behavior) seems to be to allow the colony to prey on large insects and colonies of other social insects, which would not ordinarily be vulnerable to solitary foraging workers. The myrmecophagous cerapachyines fit this psychobiological pattern well.

CLARK (1924) showed that some of the Australian *Phyracaces* hunt singly, but there seems to be little doubt that the individuals thus encountered were acting only as scouts and that the actual raids are always conducted by companies of workers. Every raid thus far recorded has involved multiple workers that were plundering the same nest at the same time and following the same raiding trail. There nevertheless remains the important distinction that CLARK has made between species that hunt (or scout) singly and those that hunt in groups. It is the author's present opinion that such a distinction may eventually prove to be a spurious one, since in the single instance where the foraging activities of a colony have been followed for any extended period of time (*Phyracaces cohici*) foraging commenced as a group activity and ended with a dispersion of solitary hunting workers. It is very likely that CLARK was merely observing different stages of the same process in the Australian *Phyracaces* he watched. We are much in need of supplementary observations of the type reported herein for *P. cohici*. Such a study could well lead to the discovery of behavior patterns and communication forms hitherto unknown in the Formicidae.

The foraging activities of the Ciu colony of *P. cohici* included some noteworthy adaptive features. In the early stages of the scouting expedition of January 2, there was marked group activity and inter-individual stimulation, which served to hasten the outward movement of the worker group as a whole and no doubt served to stimulate individual workers to join the group. The tendency observed in this colony to follow a previous raiding trail would also seem ultimately to add to the colony's

chances of finding a suitable host nest. On January 2, however, the initial group-foraging did not lead to a suitable nest, and after a time the workers began to disperse out along secondary trails of their own making, with the result that they became widely scattered in a circular area centered around the home nest. The observed behavior ended at this stage, but it is predictable that if a new host colony were located in the course of the later, dispersed phase of the foraging pattern, a raid would develop, and a new raiding trail would be established by scent deposition. This trail would then serve as the new route along which the ants would tend to forage on succeeding days. Thus a cycle can be hypothesized, incorporating the following four steps:

1. Raiding by groups of workers.
2. Establishment of a strong olfactory raiding trail by scent deposition.
3. Development of subsequent foraging and raiding along the trail until the host colony is depleted or scattered.
4. Dispersion of foraging workers from the raiding trail until a new host colony is located.

It is easy to see how such an alternation of foraging and raiding behavior might continue indefinitely and result in a highly efficient exploration and exploitation by the *Phyracaces* of the circumnidial territory.

Another matter of especial interest is the docile behavior exhibited by the ant colonies being raided by the cerapachyines. The energies of these ants seemed to be devoted entirely to rescuing and hiding their brood. There was no evidence of active resistance to the cerapachyines, although of course this could have been occurring within the host nest out of sight of the observer. It may be that such submissiveness is of ultimate advantage to the host species, in that it eliminates combat in which the host species would be at a distinct disadvantage. In actual practice the raided colonies usually survive the cerapachyine raids with a substantial part of their brood and worker population preserved intact.

### Summary.

Notes on the predatory behavior of species of *Cerapachys*, *Phyracaces*, and *Sphinctomyrmex* are given. All of the species thus far studied have proven to be myrmecophagous, feeding on the brood (and in some cases adults) of other species of ants. Raids are conducted by groups of workers and are usually of short duration. A foraging expedition of *Phyracaces cohici* is described, during which the workers started out as a compact group but later dispersed into small groups and lone individuals deployed in a circular pattern around the home nest. On the basis of these observations there is suggested a hypothetical pattern of alternating foraging and raiding behavior, which is believed to result ultimately in an efficient exploitation by the ants of the surrounding territory. Notes on other phases of biology, including colony size and nest structure, are given.

*Résumé.*

On a présenté quelques observations sur les habitudes de pillage des espèces *Cerapachys*, *Phyracaces* et *Sphinctomyrmex*. Toutes les espèces étudiées jusqu'à présent sont myrmécophages; elles dévorent le couvain — et dans certains cas les adultes — d'autres espèces de Fourmis. Les incursions sont effectuées par des groupes d'ouvrières, et sont généralement de courte durée. On décrit une expédition de fourrage de *Phyracaces cohici*, au cours de laquelle les ouvrières, parties en troupe, se dispersèrent par petits groupes et en individus isolés déployés en cercle autour de leur fourmilière. Ces observations suggèrent l'existence d'un cycle alternatif de fourrage et de razzias, ce qui permettrait aux Fourmis l'exploitation efficace des territoires avoisinants. On décrit, de plus, quelques autres aspects de la biologie de ces espèces, notamment les dimensions et le plan de leurs fourmilières.

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## NOUVELLES DE L'UNION

### TRAVAUX PUBLIÉS PAR DES MEMBRES DE L'UNION

ITO MASAHARU. — 1952. A consideration of the effective concentration of DDT and BHC emulsions for the Arctiid Moth, *Diacrisis imparilis* Butler (*Botyu-Kagaku*, 17, 88-93) (in Japanese with English summary). — 1953. Social interference of the Rust-red flour beetles, *Tribolium castaneum* [*Kagaku* (Iwanami Publ. Co. Ltd., Tokyo), 23 (7), 370-371] (in Japanese). — 1954. Experimental studies on the mechanism of aggregation formation in injurious insects. I. Some problems on the degree of aggregation with special reference to the border effects of movement of the Rust-red flour beetle [*Physiology and Ecology* (Kyoto), 6 (1), 55-62] (in Japanese with English summary). — 1955. Basic properties of social insects.—On the group effect observed in certain gregarious insects, from the view point of the comparative sociology [*Biological Science* (Iwanami Publ. Co. Ltd.), 7 (2), 67-73] (in Japanese.) — 1955 a. On the meaning of the "air-space" in the population growth of the Rust-red flour beetle, *Tribolium castaneum* (Herbst). Experimental studies on a role of behavior in the population of injurious insect. 1st. Report [*Oyo-Kontyu*, 11 (1), 25-31] (in Japanese with English summary). — 1956. Experimental studies on a role of behavior in the population of injurious insect. End report Distribution pattern of the deposited eggs of the Rust-red flour beetle, *Tribolium castaneum* Herbst [*Japanese Journal of Ecology*, 5 (3), 101-103] (in Japanese with English summary). — 1956 a. The relation between the oviposition of the Rust-red flour beetle, *Tribolium castaneum*, and its burrowing of entrance into flour (Experimental studies on a role of behavior in the population of injurious insect. 3rd. Report. Researches on Population Ecology (Entomological Laboratory, Kyoto University, 3, 16-26) (in Japanese with English summary). — 1956 b. On a form of the spacial dispersal of larval population based on the unit egg-masses of socound brood of the Rice-stem borer, *Chilo supresaris* [*Oyo-Konchu*, 12 (4), 230-231] (in Japanese). — 1957 a. Research working on a grouping life of the insects. What is the Population Ecology [*Shin-Konchu* (Hokuryukan Publ. Co. Ltd., Tokyo), 10 (2), 24-29] (in Japanese).

*Papers which were in press and prepared.*

ITO MASAHARU. — 1957. Ecological discussion on the theory to forecast insect pests [*Seitai-Konchu or Insect Ecology* (Rikusui-shya Publ. Co. Ltd., Tokyo), in press] (in Japanese with English summary). — 1957. Some problems of a research work of the dipersal behavior as a "population process" of insects (*Physiology and Ecology*, Kyoto University) (in Japanese with English summary). — 1957. Experimental studies on a role of behavior in the population of injurious insect. 4th. Report. Effects of population density against the burrowing behavior into flour by the adult beetle of Rust-red flour beetle, *Tribolium castaneum* (*Oyo-Dobutu-Konchu*) (in Japanese with English summary).

KEVAN (D. K. McE.), Dr., Zoology Section, Department of Agricultural Sciences, School of Agriculture, Sutton Bonington, *Loughborough*, Leics, G. B., **Ac. I. S.**

1943. An account of *Schistocerca flavofasciata* (De Geer 1773) in Trinidad (Orthoptera: Acrididae) (*Bull. Ent. Res.*, **34**, 291-310). — 1948. New species of *Parasphena Bolivar* 1884 (Orthoptera: Acrididae, Pyrgomorphinae) from East Africa (*J. E. Afr. nat. Hist. Soc.*, **19**, 110-130 [1946]). — 1949. A revision of the East African genus *Acrosteegas* Karsch, 1896 (Orthoptera, Acrididae, Catantopinae) (*Proc. R. Ent. Soc. Lond.* [B], **18**, 90-6). — Notes on East African Bush Locusts with special reference to *Phymataeus aegrotus* (Gerstaecker, 1869) (Orth., Acrid., Pyrgomorphinae) (*Bull. Ent. Res.*, **40**, 359-60). — 1950. Orthoptera from the Hills of South East Kenya (*J. E. Afr. nat. Hist. Soc.*, **19**, 192-221, 1 pl. [1947]). — Further records of Orthoptera from the Turkana Desert (*Ibid.*, 222-4 [1947]). — The grasshopper fauna of a small East African Swamp (*Ent. Mon. Sag.*, **86**, 316-9). — 1951. Preliminary records of some Acridoidea (Orthoptera) from remote parts of East Africa (*Ibid.*, 713-8). — 1951. An examination of the Angolan genus *Caconda* I. Bolivar, 1884 (Orthoptera, Acrididae, Pyrgomorphinae) (*Publ. cultur. Compan. Diamant. Angola*, **13**, 19-28). — *Platycleis occidentalis* Zeuner (Orthoptera, Tettigoniidae) in the Midlands (*J. Soc. Brit. Ent.*, **4**, 42-43). — 1952. A study of the genus *Chrotogonus* Audinet-Serville, 1839 (Orthopt., Acrid., Pyrgomorphinae).—I. The subgenera *Obbiacris*, nov. and *Shoacris*, nov. (*Mitt. schweiz. ent. Ges.*, **25**, 87-96). — Dermaptera, Manteodea, Phasmatodea and Saltatoria collected by Dr. B. Benzon and Dr. F. W. Braestrup in southern and central Kenya Colony (*Ent. Medd.*, Copenhagen, **26**, 222-230). — "Faune de France. 56. Orthoptéroïdes", by L. Chopard (*Ent. Mon. Mag.* **88**). — On the systematic position of two anomalous genera previously placed in the subfamily Pyrgomorphinae (Orth., Acrididae) (*Ibid.*, 265-272). — A summary of the recorded distribution of british Orthopteroids (*Trans. Soc. Brit. Ent.*, **11**, 165-180). — 1953. A new species of *Ramakrishnaia* I. Bolivar from the Nilgiris (Orthoptera: Acrididae) (*Ind. J. Ent.*, **14**, 269-272). — Notes on the distribution of British Orthopteroids (*J. Soc. Brit. Ent.*, **4**, 119-122). — "Vita di Scienziato (Biografia di Filippo Silvestri)", by Giuseppe Jannone (*Ent. Mon. Mag.*, **89**, xvi). — A new species of *Tenuitarsus* I. Bolivar, 1904, from the Sudan (Orthopt., Acrid., Pyrgomorphinae) (*Proc. R. Ent. Soc. Lond.* [B], **22**, 41-54). — An interesting new pyrgomorphine grasshopper (Orthoptera, Acrididae) in the U. S. National Museum (*J. Wash. Acad. Sci.*, **43**, 117-119). — The generic name *Dictyophorus* Thunberg, 1815 (Orth., Acrididae) (*Ent. Mon. Mag.*, **89**, 103-105). — "The Grasshoppers and Locusts (Acridoidea) of Australia. Volume I. Families Tetrigidae and Eumastacidae", by James A. G. Rehn (*Ibid.*, **19**). — The Ceylonese species of *Orthacris* I. Bolivar, 1884 (Orthoptera, Acrididae, Pyrgomorphinae) (*Spolia Zeylan.*, Colombo, **27**, 17-34). — On the identity of *Gryllus scaber* Fabricius, 1798 (Orthopt., Acrididae) (*Ent. Medd.*, Copenhagen, **27**, 482-488). — An unusual stridulatory mechanism in *Xyronotus aztecus* Sauss (Orth., Acrididae) (*Ent. Mon. Mag.*, **89**, 169-170). — 1953. The identity of *Ectobius pallens* Stephens, 1835 (Dictyoptera, Blattodea) (*Entomologist*, **86**, 169-171). — An unusually massive termitarium from the Ogaden (*Entomologist*, **86**, 166-167). — The status of *Tetrix bipunctata* (Linn.) (Orthoptera, Tetrigidae) in Britain (*Ent. Gaz.*, **4**, 205-224). — "Australian Termites: The Biology, Recognition, and Economic Importance of the Common Species", by F. N. Ratcliffe, F. J. Gray and R. T. Greaves (*Ent. Mon. Mag.*, **89**, 39). — On the gender of the generic name *Ommexecha* Serville, 1831, and the correct rendering of the same *Chrotogonus homalodemus* (Blanchard, 1836) (Orth., Acrididae) (*Thid.*, 221-223). — "Fauna SSSR. Tom. IV. Vyp. 2. Nasekomyye Pryamokrylye. Sarancheyye (Catantopinae)", by L. L. Mishchenko (*Ibid.*, 35). — Some difficulties raised in applying the rule of priority to supra-generic nomenclature, as illustrated by the name Pyrgomorphinae (Insecta: Orthoptera) and its alternatives. Communication read at the XIVth. International Congress of Zoology, Copenhagen, 6th. August., 1953 (*Spec. Pap. Univ. Nottm. Sch. Agric. Zool. Sect. i: ii + 11 pp.* [mimeo]). — Preliminary list of the Mantodea of Trinidad, B. W. I., (*Ann. Mag. nat. Hist.* [12], **6**, 809-816).

— A teratological specimen of *Taphronota calliparea* Schaum (Acrididae) (*J. Ent. Soc. ethn. Africa*, 16, 139-140). — Additional notes on the distribution of British Orthopteroids (*J. Soc. Brit. Ent.*, 4, 183-185). — 1954. "Grasshopper Glacier of Montana and its relation to long-distance flight of grasshoppers", by A. B. Gurney (*Ent. Mon. Mag.*, 90, 3-4). — "The Grasshoppers and Locusts (Acridoidea) of Australia. Vol. II. Family Acrididae (Subfamily Pyr Gomorphinae)", by James A. G. Rehn (*Ibid.*, 7-8). — A note on the Acrinid subfamily dame Catantopinae (*J. Soc. Brit. Ent.*, 4, 223-225). — Blattodea from Northern Kenya and Jubaland (*Ann. Mag. nat. Hist.* [12] 7, 166-167) (co-author with Prof. L. Chopard, Paris). — Mantodea from Northern Kenya and Jubaland (*Ibid.*, 455-473). — Orthoptera-Caelifera (other than Acrididae) from Northern Kenya and Jubaland (*Opusc. Ent., Lund.*, 19, 44-54). — Pyrgomorphine Acrididae from J. W. Zetterstedt's Insecta Exotica collection (*Ibid.*, 78). — Ueber Färbung und Sicheingraben von *Acrotylus junodi* (Schulthess) (Orth. Acrid., Oedipodinae) (*Veröff. Ueberseemus. Bremen* [A], 2, 213-226 + 1 pl) (co-author with Dr. Knipper, Bremen). — "Unorthodox" methods of sound production in the Orthoptera (*Spec. Pap. Univ. Nottm. Sch. Agric. Zool. Sect.*, 2, 22 pp. [mime]). — A study of the genus *Chrotogonus* Audinet-Serville, 1839 (Orthoptera, Acrididae): I. Preliminary notes on synonymy and distribution in the Belgian Congo and adjacent territories (*Ann. Mus. Congo, Tervueren, in-4°* (Zool.), 1, 446-456). — Dermaptera from Northern Kenya (*Entomologist*, 87, 75-76). — Phasmatodea from Northern Kenya (*Ibid.*, 112-116) (co-author with Prof. L. Chopard, Paris). — The Taxonomy, Phases, and Distribution of the Genera *Chorteicetes* Brunn. and *Austroicetes* Uv. (Orthoptera, Acrididae), by K. H. L. Key (*Ent. Mon. Mag.* 90, 35). — Orthoptera-Ensifera from Northern Kenya and Jubaland (*Trans. R. Ent. Soc. Lond.*, 105, 315-353) (co-author with Prof. L. Chopard). — A study of the genus *Chrotogonus* Audinet-Serville, 1839 (Orthoptera, Acrididae). III. A review of available information on its economic importance, biology, etc. (*Ind. J. Ent.*, 16, 145-172). — Further notes on the distribution of British Orthopteroids (*Proc. Soc. Brit. Ent.*, 5, 65-71). — Sound Production and Reception in Orthoptera (*Ent. Rec.*, 66, 257-260). — "Pryamokrylye, Tom. II, Wyp. 2. Kuznechikovyje. Podsem. Listovye Kuznechiki (Phaneropterinae)." Fauna SSSR, Novaya Seriya No. 59 [Orthoptera Vol. II, Section 2. Bush-cricket. Subfam. Leaf Bush-cricket (Phaneropterinae). Fauna of the U. S. S. R., n.s. no. 59]. By G. Ya. Bei-Bienko (*Ent. Mon. Mag.*, 90, 47-48). — 1955. Two allied Orthopteroid insects from Edinburgh (*Ent. Rec.*, 67, 35-36) (co-author with E. Dunn). — A new species of Eneopterid cricket (Orth. Grylloidea) imported into Britain (*Ent. Mon. Mag.*, 91, 1-3, pl. I). — A further contribution to our knowledge of the Acrididae (Orthoptera) of Angola (*Publ. cult. Compan. Diamant. Angola*, 24, 61-82). — Méthodes inhabituelles de production de son chez les Orthoptères (*Ann. Epiphyt.*, 1954 [suppl.], 103-141) (fasc. hors série). — Mole-Crickets in Britain (*Ent. Rec.*, 67, 91-91). — A note on the name of the common house Cricket, *Acheta domesticus* (Orthoptera, Gryllidae) (*Ent. Mon. Mag.*, 91, 108-109). — Cockroaches (Blattariae) from Trinidad B.W.I. with a few records from other parts of the Caribbean (*Opusc. Ent., Lund* [co-author Dr. K. Princis, Lund] 20, 149-169). — Zur Biologie, Systematik, Morphometrie und insbesondere Schwarmbildung Afrikanischer *Homorocoryphus* (Orth. Tettigon Conocephalidae) (*Veröff. Ueberseemus. Bremen* (A), 3, 277-318, pl. I) (co-author Dr. H. Knipper, Bremen). — 1954 a. On the subdivisions of the genus "*Gryllus*" Linnaeus, 1758 (*Opin. Declar. Internat. Commiss. zool. Nomencl.*, 8, 229-231). — 1955 (contd.). A further note on the Mole-Cricket (*Gryllotalpa*) (*Ent. Rec.*, 67, 211-212). — A new subspecies and two little-known East African species of the genus *Catantops* Schaum, 1853 (sens. lat.) (Orthoptera, Acrididae) (*Entomologist*, 88, 199-203). — East African Blattodea, Phasmatodea and Orthoptera (Ergebnisse der Deutschen zoologischen Ostafrika Expedition 1951-1952, Gruppe Lindner, Stuttgart, Nr. 5) (*Boitr. Ent.*, Berlin, 5, 472-485). — The Home of the House Cricket *Acheta domesticus* (L.) (Orth. Gryllidae) (*Ent. Mon. Mag.*, 91, 263). — The Gender of the Genus *Acheta* Fabricius (Orth., Gryllidae) (*Ibid.*, 91, 310). — 1956. New East African Acrididae (Orthoptera) (*Ann. Mag. nat. Hist.* [12], 9, 20-35). — Fightless



African Genera of Pyrgomorphine Grasshoppers allied, or superficially similar, to *Parasphona* I. Bolivar, 1884, and *Pyrgomorphella* I. Bolivar, 1904, with Descriptions of certain new forms (Orthoptera, Acrididae) (*Publ. cult. Compan. Diam. Angola*, 29, 107-134). — Results from the Danish Expedition to the French Cameroons 1949-1950-XV. Orthoptera, Acrididae (*Bull. Inst. fr. Afr. noire*, 18 [A], 960-977). — The known distribution of British Orthopteroids, Fourth Supplement (*J. Soc. Brit. Ent.*, 5, 187-192). — Massive Termitaria in the Ogaden (*Proc. XIV. Internat. Congr. Zool.*, Copenhagen, 1953, 498). — 1957. Wiltshire Orthopteroids (*Entomologist*, 90, 12-16). — "Annotated Catalogue of African Grasshoppers", Compiled by H. B. Johnston (*Ent. Mon. Mag.*, 93, 7-8). — A Study of the genus *Chrotogonus* Audinet-Serville, 1839 (Orth., Acridoidea). IV. Wing Polymorphism, Technical Designations and Preliminary Synonymy (*Tijdschr. Ent.*, Leiden, 100, 43-60). — Zur Kenntnis der Gattung *Chrotogonus* Audinet-Serville, 1839. Erste Beobachtungen über das Sicheingraben (Orthoptera, Acrididae, Pyrgomorphinae) (A Study of the Genus *Chrotogonus* Audinet-Serville, 1839. V.) (*Zschr. Tierpsychol.* [in press]) (co-author Dr. Knipper, Bremen). — Orthoptera-Caelifera from Northern Kenya and Jubaland. II. Pamphagidae, Pyrgomorphidae, Lentulidae and Romaleinae (*Opusc. Ent.*, Lund, 21 [in press]).

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# MODIFICATIONS A LA LISTE DES MEMBRES PARUE DANS LE NUMÉRO 1 DU TOME IV, JANVIER 1957

## *New members.*

- BLACKITH (R. E.), Dr. Imperial College Field Station, *Sunninghill*, Berks., G.-B.,  
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U. R. S. S.
- PAYLOVSKY (E.), Directeur Institut de Zoologie, Académie des Sciences de l'U. R. S. S.,  
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- WINOGRADOWA (T.), Professeur, Institut vétérinaire, *Léninegrad*, rue de l'Académicien  
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## *New address.*

- AYRE (G. L.), Andlawstrase 7, *Freiburg-Br.*, DE, **F.**
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- WEIR (J. S.), Zoology Department, University College of Rhodesia and Nyasaland, P. B.  
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For further information write to the address below:

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